Impact of fire on tussock grassland invertebrate populations

Department of Conservation
Te Papa Atawhai

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Cover: A smouldering summer burn plot at Mount Benger. *Photo: Barbara Barratt.*

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ABSTRACT

The invertebrate fauna of tussock grassland in New Zealand has not been well studied, and the effect of burning on the biodiversity of the ecosystem is poorly understood by land managers. The impacts of burning on two tussock grassland invertebrate communities in Otago, New Zealand, were investigated between 1998 and 2006. At each site, three replicate 1-ha plots that were unburned (control), or burned in spring or summer were sampled. Pre- and post-burn sampling compared invertebrate densities and trophic group structure in inter-tussock (turf) and tussock samples, and recovery after treatment. Most groups were initially reduced in density post-burn. In the 1–2 year period following treatment, Thysanoptera and Hemiptera 'rebounded' and reached significantly higher population densities than before the fires. By the end of the study, Amphipoda had not recovered to pre-burn densities. In general, herbivore population densities recovered over a 2–3 year period, and litter-dwelling invertebrate population densities were most negatively impacted. Season of treatment had no major impact on invertebrate responses. Coleoptera were chosen as a representative group for more detailed investigations of responses at species level. Coleoptera species richness was reduced by about 50% at 2–3 months post-burn, but recovered to pre-burn levels 3 years later. There was no evidence of a change in the density of exotic Coleoptera following the burning treatments. Invertebrate data from these sites should be considered as case studies, rather than applicable to tussock grassland in general. However, these findings have several implications for the management of tussock grassland: fire treatments that remove the litter layer are likely to reduce litter-dwelling invertebrate populations for 3 years or more; summer fires do not appear to be more detrimental to the invertebrate community than burning in spring, based upon the limited seasonal data available to us; and the exotic component of the fauna does not increase in response to fire in the first 3–4 years after burning.

Keywords: tussock grassland, invertebrates, Coleoptera species, burning, fire, diversity, recovery, exotic species, New Zealand

1. Introduction

Grasslands of indigenous tussock species are characteristic of the lower rainfall hill and high country areas in the South Island of New Zealand, and are used for extensive pastoralism (Floate 1992). Since European settlement in the late 19th century, fire has been used extensively to facilitate movement of grazing animals and to convert tussock grassland into improved pasture. Burning promotes new tussock growth, which is palatable to stock. It also removes litter to increase the success of aerial over-sowing with introduced legumes and grasses (Lowther & Douglas 1992). For pasture management, burning is usually carried out in spring, when conditions are relatively cool and the soil and vegetation are moist. Accidental fires tend to occur in late summer, when conditions are usually drier, and hence the damage to vegetation and litter would be expected to have a more severe impact on invertebrates.

There are concerns that fire damages native biota, allows weeds to establish and promotes soil erosion (Payton & Pearce 2001). Overuse of fire in tussock grassland has been recognised as causing loss of tall tussock species, with their replacement by short tussock species or invasive weeds such as *Hieracium* (Aspinal 2001). Local agencies with responsibility for promoting sustainable land use have pointed out that the burning of tussock grassland can accelerate soil erosion and reduce soil quality, change vegetation characteristics, reduce conservation values and habitats for flora and fauna, and reduce water yield (Otago Regional Council 2002).

Since 1983, considerable areas of tussock grassland have been retired from grazing and formally protected as a result of the Protected Natural Area Programme, which sought to protect representative vegetation types from 85 biogeographic areas (ecological regions) across the country (McEwen 1987). As a result of the crown pastoral tenure review under the Crown Pastoral Land Act 1998, areas of rangeland, particularly at higher altitudes, are currently being retired from grazing and managed so that their natural character and the indigenous biodiversity will be retained, and in some cases restored. In order to maintain conservation values of these areas, an improved understanding of the biodiversity and dynamics of grassland ecosystems is required.

Land managers need information about the impact of fire on the conservation values of tussock grassland to make appropriate management decisions for these areas. Hunt (2007) expressed the view that the Department of Conservation (DOC) needs to improve monitoring of changes to ecosystems after fire. Hunt's report acknowledged the research outlined in this study, but recommended that continued research on impacts of fire on ecosystems and biodiversity be given a high priority, 'especially invertebrates before and after fires'.

1.1 BACKGROUND

Worldwide, research into the impacts of fire on invertebrates in grassland environments have shown few consistent patterns (Tscharntke & Greiler 1995; Friend 1996; Blanche et al. 2001). Responses to fire depend upon seasonal and environmental factors and their interaction with the micro-habitat requirements of the fauna. Warren et al. (1987) and Webb (1994) attributed reductions in densities of some arthropods to the reduced levels of soil moisture and changes in microclimate that follow removal of the litter layer. Fire intensity is important in determining impacts on invertebrates (Swengel 2001), and this is influenced by several factors, including fuel load, vegetation moisture content, weather conditions and topography. However, even after very hot and 'complete' burns, mortality of invertebrates has rarely been reported to be 100% (Swengel 2001). The size and uniformity of the burnt area naturally influences the rate of recolonisation from surrounding unburnt areas, or unburnt patches within the burnt area. The impact of fire can also vary for different invertebrate life-cycle stages; for example, a soil-dwelling stage is likely to be less immediately affected by fire than a surface-dwelling stage.

Warren et al. (1987) reviewed literature on the impact of fire on each major taxonomic group found in grassland. Studies investigating the effect of fire on invertebrates are full of conflicting and variable data. This is partly because the studies have been carried out using different methods, with widely differing treatment intensities and regularities, and in areas with different climates. Furthermore, many studies reported in the literature have been carried out in ecosystems that are fire-adapted, and thus are likely to have different responses from essentially non-fire-adapted environments such as New Zealand tussock grassland. Warren et al. (1987) found that litter-dwelling invertebrates such as mites and Collembola are generally adversely affected by fire as a result of loss of the litter layer where they live and feed. Miriapods, such as millipedes and centipedes, were less susceptible to acute impacts because of their cryptic behaviour, but it was found that post-burn habitat modification could reduce populations. Impacts on some of the larger groups, such as Coleoptera, Diptera and Hemiptera, were found to be very variable, depending upon their trophic group and the seasonal characteristics of the fire. Ants, which are common in most grassland environments, usually survived the acute impacts of fires, and generally recolonised burnt areas rapidly.

Several studies in New Zealand have investigated the impact of tussock burning on plant communities (e.g. O'Connor & Powell 1963; Mark 1965; Payton et al. 1986), but comparatively little has been published on the effect of indigenous grassland burning on invertebrates. Yeates & Lee (1997) found that 18 months after a spring burn densities of both mites and Collembola in litter and in up to 2 cm soil depth were about 50% of those in an adjacent unburnt area; however, after 30 months, the densities of these groups in the burnt areas were < 10% of the unburnt areas. Henig-Sever et al. (2001) found, not unexpectedly, that litter-dwelling invertebrates are more severely affected by fire than those living deeper in the soil profile and suggested that inhabitants of the litter layer might be useful ecological indicators of fire intensity on ecosystems.

In 1960, the Tussock Grasslands and Mountain Lands Institute (TGMLI) was set up to assist farming in tussock grassland, and Graeme White, employed by the TGMLI, emphasised the importance of understanding insect population dynamics if management was to be successful (White 1972). Invertebrate biodiversity and ecology in tussock grassland in Otago is not well known, although the body of knowledge is steadily increasing. As for the New Zealand invertebrate fauna in general, studies have indicated that the fauna exhibits a high degree of endemism. One of the earliest papers on tussock grassland insects reported on a study in Canterbury, where damage to tussock plants from noctuids and other Lepidoptera was described, and *Odontria* (Coleoptera: Scarabaeidae) larvae were found to be killing patches of grasses (Dick 1940). The author noted that run-holders believed that burning tussock in spring reduced the numbers of caterpillars found in tussock plants.

In 1978, the senior author was appointed to work on tussock grassland entomology in Otago. The work, as in Canterbury, was mainly applied with emphases on the ecology and management of the striped chafer (*Odontria striata* White), and pests of white clover (*Trifolium repens* L.) seedlings oversown into tussock. Research on these two topics was prompted by the concerns of farmers and researchers, respectively, and the studies resulted in a series of publications (Barratt 1982a, b, 1983; Barratt & Campbell 1982; Barratt & Johnstone 1984; Barratt & Lauren 1984). However, it was Brian Patrick, a well-known lepidopterist, who really laid the foundation for our current knowledge of tussock grassland insect biodiversity and ecology, by instigating a series of collecting trips with colleagues to tussock grassland sites throughout Otago and Southland, which resulted in a series of reports and publications (Patrick et al. 1984, 1985a, b, 1986, 1993a, b, 1987; Barratt & Patrick 1987; Patrick & Barratt 1988, 1989; Patrick 1991, 1994; Dickinson et al. 1998).

Since then, there have been a number of students at the University of Otago, Dunedin, under the guidance of Prof. Katherine Dickinson, who have focussed their ecological studies on tussock grassland, some of whom have used the sites that are the topic of this report (Derraik et al. 2001, 2002, 2003; Murray 2001; Goodman 2002; Murray et al. 2003, 2006; Dixon 2004; Rate 2005; Scott 2007). Recently, a student at Lincoln University, Christchurch, has initiated a PhD study of spiders at the Deep Stream site.

Since we still know so little about the composition of tussock grassland invertebrate communities, we use Coleoptera as a surrogate group in this report. Coleoptera are a suitable group for this because they are speciose, they include representatives of all trophic groups and they are reasonably well known taxonomically (Hutcheson et al. 1999). Furthermore, Bulan & Barrett (1971), working in cereal plots in Ohio, USA, found that the responses of Coleoptera to fire were representative of the rest of the arthropod community, and reported that changes in biomass and species diversity were good measures for evaluating the impact of fire.

1.2 OBJECTIVES

The objective of the project was to provide information to assist in the future management of natural grassland ecosystems. This included information on:

- The short- to medium-term (3 months up to 4 years) impacts of burning on the density of tussock grassland invertebrates
- The short- to medium-term impacts of burning on Coleoptera species density, species richness, species diversity and trophic structure
- The time frame over which the invertebrate fauna in tussock grassland is able to recover to an equilibrium density after burning
- The time frame over which the Coleoptera fauna is able to recover to pre-burn species densities, species richness and species diversity after burning
- The comparative short- to medium-term impact of tussock burning in moist spring conditions compared with those in hot, dry summer conditions
- The extent to which exotic Coleoptera species have established in native tussock grassland and their responses to burning

2. Methods

2.1 SITES

Two sites in the Otago region of the South Island of New Zealand were chosen for this study: Deep Stream (DS) and Mount Benger (MB) (Fig. 1). These sites are part of a multi-disciplinary study of fire modelling (Scion study), and the impacts of tussock burning on plant (Payton & Pearce 2009) and invertebrate (present study) communities. They were chosen as representatives of higher (MB) and lower (DS) altitude tussock grassland environments in Otago. They were selected on the basis of their relatively undisturbed soils (no history of cultivation) and relatively unmodified vegetation. Both sites had experienced fires since European settlement, but had not been burned for at least 10 years before these experimental burns. Site details are given in Table 1.

TABLE 1. A. SITE AND B. SOIL CHARACTERISTICS AT DEEP STREAM AND MOUNT BENGER STUDY SITES.

A

SITE CHARACTERISTIC	DEEP STREAM	MOUNT BENGER
Tenure	Dunedin City Council water reserve	Benger Pastoral Lease
Altitude	640–700 m a.s.l.	1100–1180 m a.s.l.
Map reference	45°44′S 169°54′E	45°58′S 169°26′E
Dominant vegetation*	*Chionochloa rigida*	*Chionochloa rigida*
	Gaultheria nana	*Poa colensoi*
	Poa pratensis	*Polytrichum juniperinum*
	Poa colensoi	*Agrostis capillaris*
Slope and aspect	<10° predominantly N	2 plots flat; 1 plot <20° S
Mean annual rainfall[†]	993 mm	1264 mm
Soil type[‡]	Wehenga silt loam	Carrick
	Allophanic brown soils	Allophanic brown soils

* Espie & Barratt (2006). 	 ‡ Hewitt (1992).
† Payton & Pearce (2009).

B

SOIL CHARACTERISTIC*	DEEP STREAM		MOUNT BENGER	
	TURF	TUSSOCK	TURF	TUSSOCK
% organic C	7.1	7.9	7.7	7.3
% organic matter	12.2	13.6	13.3	12.6
Total % N	0.38	0.42	0.43	0.47
C:N ratio	19	19	18	16
pH	4.6	4.6	4.6	4.5
Ca (me/100g)[†]	125	125	125	125
P (µg/g)	8	8	7	8
K (me/100g)[†]	80	100	60	60
Mg (me/100g)[†]	45	55	35	40
Na (me/100g)[†]	15	20	15	15

* Sarathchandra et al. (2005). 	 † Milli equivalents per 100 g soil.

Figure 1. Map of the study sites at Deep Stream and Mount Benger (from Payton & Pearce 2009).
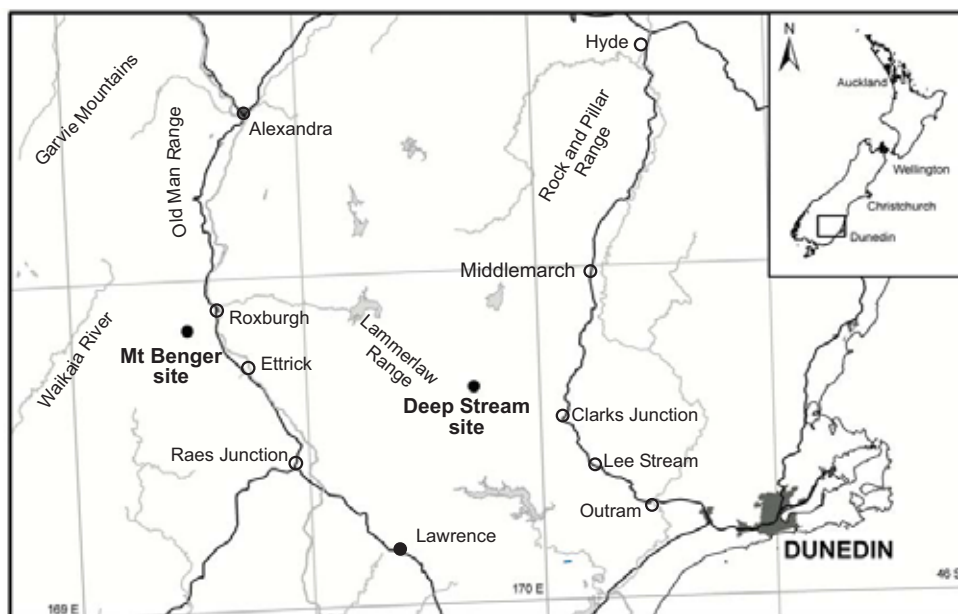
2.2   TREATMENTS

At each site, nine 1-ha plots were randomly allocated to three replicates of three treatments: control (unburnt), burned in spring or burned in summer/autumn (these will be referred to as spring-burnt and summer-burnt plots, respectively). Each plot was marked out into twenty-five 20×20 m sub-plots. One of these sub-plots in each main plot was randomly selected for invertebrate sampling, excluding the outer sub-plots, which served as a buffer to reduce 'edge effects'. For simplicity, the sub-plots designated for invertebrate sampling will henceforth be called invertebrate plots.

Fire treatments were coordinated, carried out and supervised by DOC staff according to best practice guidelines. Timing was based on information from the national Rural Fire Authority network of fire weather stations. Data from these stations were used to calculate a number of indices using the New Zealand Fire Weather Index System (Van Wagner 1987), which were then used to determine optimum times for burns. The burn dates, between November 2000 and April 2006, are shown in Table 2. More details of the indices used in relation to the fires for this trial are given in a report by Forest Research (NZ Fire Research 2001). The summer burn treatment at MB was delayed until March 2006 because of restrictions on burning in a prohibited fire season. The data from this treatment are not included in this report.

TABLE 2. TREATMENT AND SAMPLING DATES AT DEEP STREAM AND MOUNT BENGER.

× = pre-burn sample; **×** = post-burn sample.

TREATMENT/ SAMPLE	DATE	PLOT								
		1	2	3	4	5	6	7	8	9
Deep Stream										
Control		×					×	×		
Spring burn	2 Oct 2001			×	×				×	
Summer burn	7 Mar 2001		×			×				×
Samples	3 Apr 1998	×	×	×	×	×	×	×	×	×
	19 Aug 1998	×		×	×		×	×	×	
	11 Jan 1999	×	×	×	×	×	×	×	×	×
	14 Sept 1999	×		×	×		×	×	×	
	6 Jan 2000	×	×	×	×	×	×	×	×	×
	18 Sept 2000	×		×	×		×	×	×	
	12 Jan 2001	×	×	**×**	**×**	×	×	×	**×**	×
	9 Mar 2001	×	**×**			**×**	×	×		**×**
	24 Sept 2001	×		**×**	**×**		×	×	**×**	
	5 Oct 2001	×		**×**	**×**		×	×	**×**	
	11 Jan 2002	×	**×**	**×**	**×**	**×**	×	×	**×**	**×**
	17 Jan 2003	×	**×**	**×**	**×**	**×**	×	×	**×**	**×**
	6 Jan 2004	×	**×**	**×**	**×**	**×**	×	×	**×**	**×**
	11 Jan 2005	×	**×**	**×**	**×**	**×**	×	×	**×**	**×**
Mount Benger										
Control			×		×			×		
Spring burn	3 Nov 2000	×					×			×
Summer burn	31 Mar 2006			×		×			×	
Samples	15 Apr 1998	×	×	×	×	×	×	×	×	×
	26 May 1998	×	×	×	×	×	×	×	×	×
	13 Jan 1999	×	×	×	×	×	×	×	×	×
	20 Sept 1999	×	×		×		×	×		×
	7 Jan 2000	×	×	×	×	×	×	×	×	×
	20 Sept 2000	×	×		×		×	×		×
	10 Nov 2000	**×**	×		×		**×**	×		**×**
	15 Jan 2001	**×**	×	×	×	×	**×**	×	×	**×**
	14 Jan 2002	**×**	×	×	×	×	**×**	×	×	**×**
	8 Jan 2003	**×**	×	×	×	×	**×**	×	×	**×**
	16 Jan 2004	**×**	×	×	×	×	**×**	×	×	**×**
	Jan 2005	**×**	×	×	×	×	**×**	×	×	**×**
	Apr 2006		×	**×**	×	**×**		×	**×**	

2.3   INVERTEBRATE SAMPLING

Invertebrate sampling dates for each site are shown in Table 2. Not all invertebrate plots were sampled on each sampling date; for example, where a spring burn had been carried out, only the control and spring-burnt plots were sampled, and not the plots to be burned in summer. Invertebrates were sampled quantitatively using a 320 × 320 mm quadrat (0.1 m^2) as a guide and cutting turves with a spade to a depth of approximately 50 mm. The invertebrates extracted from these samples (see below) provided a measure of density (number/m^2). For each sample date (Table 2), twenty 0.1-m^2 inter-tussock ('turf') samples were taken by throwing the quadrat and cutting turves in a general pattern of four rows of five turves from within the invertebrate plots. In addition, in each invertebrate plot, nine samples (three rows of three) were taken as above, but which included a tussock (*Chionochloa rigida*) plant ('tussock samples'). Thus, on a date when all plots were sampled, a total of 180 turf samples and 81 tussock samples were taken from each site. Care was taken to avoid resampling areas that had been sampled previously.

All samples were individually bagged, transported to AgResearch Invermay, and stored at 4°C for a maximum of 3 weeks before processing (Bremner 1988).

2.4   INVERTEBRATE EXTRACTION AND PROCESSING

In the laboratory, invertebrates were extracted from each turf sample over a 7-day period using modified Tullgren funnel heat extractors (Crook et al. 2004). Sample extraction was arranged to avoid differential storage of treatments and plots. After extraction from turves, the invertebrates were stored in 70% ethanol at 4°C until sorting.

Samples were washed through fine muslin, which retained all invertebrates but allowed fine silt to pass though. The 'cleared' samples were then sorted and invertebrates counted under a 6.3–40× binocular microscope. A list of the 55 taxonomic groups into which invertebrates were identified is shown in Appendix 1, which also gives common names where possible. The only groups not identified and counted for each sampling date were Collembola and Acari, although for some dates these have been further subsampled and identified to family (Barratt et al. 2006); the Collembola and Acari from all other dates have been retained for future study.

Coleoptera were identified to species, so that further analysis at species level (species richness/diversity) could be carried out on a representative insect group. Adult Coleoptera were identified to morphospecies (recognisable taxonomic units) or, where possible, to species level. Larval Coleoptera were identified to family, but identification beyond this was rarely possible. In the Coleoptera species analyses, larval morphospecies are included as separate taxa even though this is likely to over-estimate species numbers. This is because it is impossible in most cases to match larvae with adults, and this also allows for the fact that larvae and adults are sometimes in different trophic groups, occupying different niches and in general performing different functions in the community.

The higher taxonomic groups were allocated to the functional categories of herbivores, carnivores, fungivores and detritivores. Carrion-feeders (Coleoptera: Dermestidae) were also present, but at densities too low to be worthwhile including in the analyses. In some cases where taxa comprised either sub-groups that varied in feeding characteristics (e.g. Lepidoptera larvae can be herbivores or detritivores), or where adults and larvae belonged in different groups (e.g. Lepidoptera again, where adults are often nectar feeders), a judgement was made on the predominant function for the particular taxon. Trophic group could not always be allocated with complete confidence, but the literature was consulted as far as possible to assist (e.g. Klimaszewski & Watt 1997).

A species list for Coleoptera from both sites is shown in Appendix 2, along with their native/adventive status and allocation to trophic group. The higher taxonomic classification of Leschen et al. (2003) was used for guidance on native/exotic status, although this was not available at the species level.

The January 2001 tussock Coleoptera samples for DS were identified for the spring-burnt plots but not for the control and summer-burnt plots. Regrettably, this omission was discovered too late to be rectified and limits our scope for data analysis for that date.

All invertebrate material has been stored fully labelled in 70% ethanol. The material identified to major groups has been separated and stored in vials. Collembola (springtails) and Acari have been stored together with the material retained by the muslin after filtering.

2.5 STATISTICAL ANALYSES

Invertebrate density data and the proportion of individuals in each trophic group were analysed for each site using restricted maximum likelihood (REML, which is a method for fitting linear mixed models producing unbiased estimates of variance) to model the effect of treatments and dates and their interactions on the $\log_e$ counts of number of individuals (Payne et al. 2006).

For the more detailed analyses of coleopteran species density data, a similarity matrix for the nine plots from DS and six plots (three replicates of control and spring-burnt plots) from MB was calculated using a Euclidean metric (which was considered appropriate since distance measures are on a continuous rather than a discontinuous scale). From this, a distance matrix (using distances between the individual plot data points) was obtained as $(2(1 - \text{similarity}))^{0.5}$. This was used for non-metric multidimensional scaling (MDS) using two dimensions (Payne et al. 2006) for Coleoptera species density data to obtain a visual assessment of the degree of similarity between the sites, and the treatment plots within the sites.

Coleopteran species richness (number of species present per plot) was calculated for the turf and tussock samples for each plot at each site on each date. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions on the $\log_e$ species richness counts (Payne et al. 2006).

Coleopteran species diversity was examined by calculating Shannon-Wiener indices of diversity (H) for each plot at each site on each date. This index is probably the most commonly used measure of biodiversity, and takes into account the number of species and the number of individuals of each species in the sample. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions on the indices (Payne et al. 2006). Changes in coleopteran species diversity following burning treatments were also investigated using k-dominance plots. These plots were used in addition to the Shannon-Wiener index because they give a good visual appreciation of the data showing all data points and the shape of the curve provides an indication of dominance (steep plots) or evenness (shallow curves) of species assemblages. Log_{10} density was ranked for Coleoptera species and plotted against cumulative percentage density. This produced curves in which the most diverse samples appear on the lower part of the plot. The pre-burn and post-burn data were compared for the same plots for DS and MB spring-burnt turf plots and for DS summer-burnt turf plots. Comparisons were not possible for DS summer-burnt tussock plots, as the pre-burn data were not available. There are no pre-burn and post-burn comparisons for the MB summer-burnt plots because of the late date (31 March 2006) of the MB summer burn.

The percentage of Coleoptera in each of five trophic groups and the percentage of exotic Coleoptera species were calculated for each plot at each site on each date. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions.

3. Results

Between April 1998 and April 2006, a total of 6177 0.1-m^2 samples were taken from the nine 1-ha treatment plots at DS and MB. Approximately 1.26 million invertebrates were extracted, identified and counted from the samples collected.

Two burn treatments were successfully undertaken on treatment plots at DS in March (summer burn) and October (spring burn) 2001. At MB, the spring burning treatment was carried out in November 2000. However, as noted above, it was not possible to conduct the summer burn at MB until March 2006.

3.1 DEEP STREAM VERSUS MOUNT BENGER INVERTEBRATE COMMUNITIES

At DS, the mean density of all invertebrates in control plots over the study period was 4018 individuals/m^2 in turf samples and 3059 individuals/m^2 in tussock samples. The equivalent mean values at MB were 2309 individuals/m^2 and 2644 individuals/m^2, respectively.

3.1.1 Taxonomic composition

At the higher taxonomic levels (i.e. order and above), the composition of the communities at the two sites was similar, with the exception of Hymenoptera (mainly ants), which were present at a higher density at DS than at MB (Fig. 2). Hymenoptera occurred at a higher density than any other group at DS, with their mean density in turf samples (averaged across all control plot samples throughout the study) reaching >1100 individuals/m^2. This was almost 30% of all the invertebrates present in the DS turf samples. At MB, the hymenopteran population was ranked at the fifth highest density; the Myriapoda were recorded at the highest density (348 individuals/m^2), although densities here were lower than at DS (Fig. 2).

At DS, turf and tussock samples contained similar densities of the different invertebrate groups, with the exception of Hymenoptera, which were present at a far greater density in the turf than the tussock samples. Myriapoda densities were higher than other groups in tussock samples at DS. At MB, the greatest difference between turf and tussock samples was in the density of Hemiptera; the Pseudococcidae was by far the largest family in this group in terms of number of individuals, and their density was higher in the tussock samples than in turf samples.

Notes on a few of the taxa collected and their ecology are given in Appendix 3.

Figure 2. Mean density of
invertebrates (no. individuals/
m² at Order level or above
in control plots for all sample
dates shown for turf and
tussock samples.
A. Deep Stream; B. Mount
Benger. Error bars represent
2 SEMs.

Figure 2. Mean density of invertebrates (no. individuals/m²) at Order level or above in control plots for all sample dates shown for turf and tussock samples. A. Deep Stream; B. Mount Benger. Error bars represent 2 SEMs.
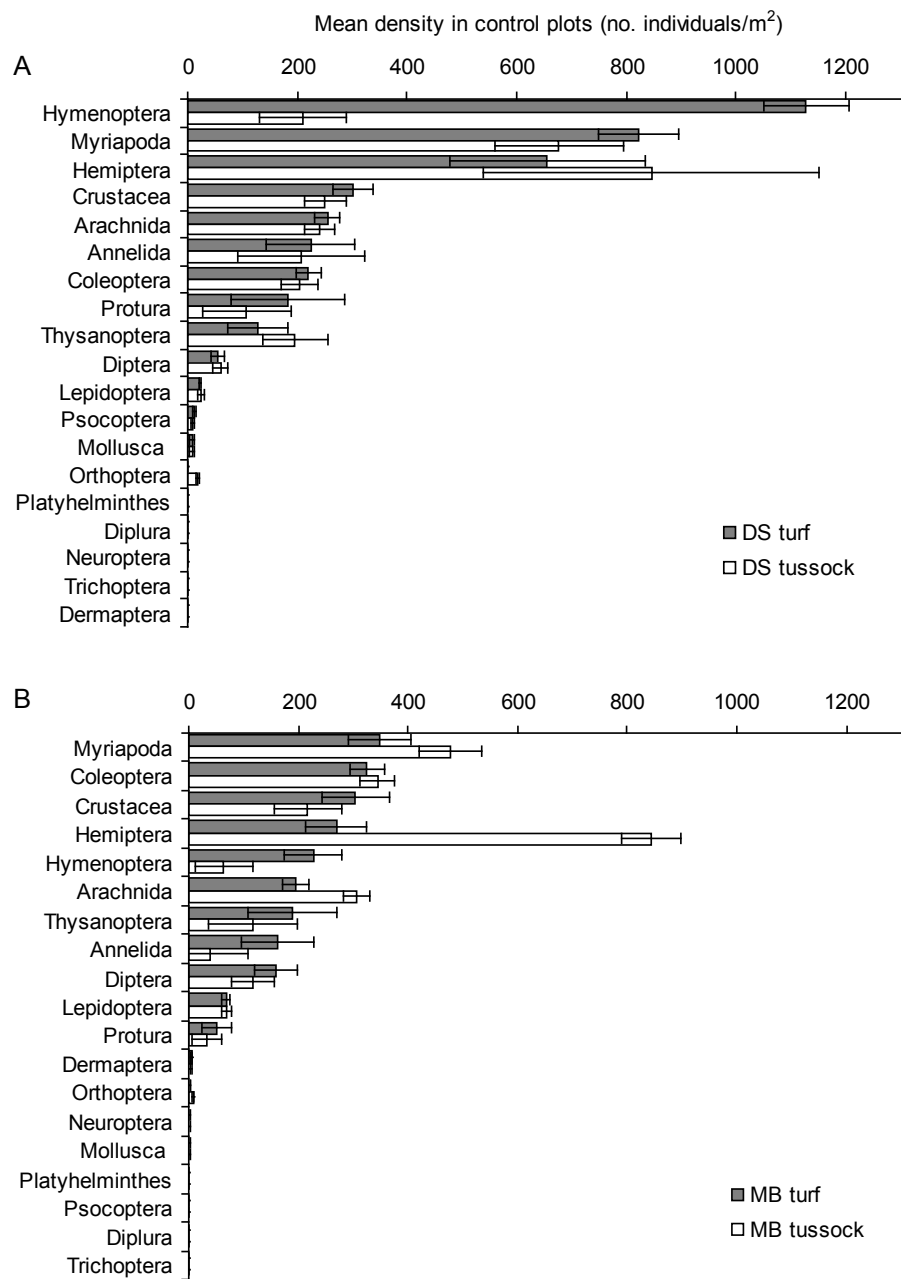
3.1.2 Trophic composition

The mean density of each of the four recognised trophic groups was calculated for each site and vegetation sample type for control plots as an average of all sample dates. Formicidae (ants) were excluded from this analysis because they are generalist feeders. For each site and vegetation type, herbivores comprised 30–40% of the total invertebrate density, carnivores 20–25%, detritivores 30–40%, and fungivores about 5% (see section 3.3).

3.2 EFFECT OF BURNING TREATMENTS ON INVERTEBRATE DENSITY

The effect of the spring and summer tussock fires on total invertebrate density and on Coleoptera density is shown in Fig. 3 (DS) and Fig. 5 (MB) in the sections that follow. Effects on other taxa that were present at high densities and are discussed in the sections below can be found in Appendices 4 and 5. The probabilities calculated for the restricted maximum likelihood model for treatment effects (Chi P) are shown in Table 3, and comments on significant differences for individual dates are provided where they occurred. Data for Platyhelminthes, Neuroptera, Mollusca, Trichoptera and Dermaptera are not shown in Table 3 because in most cases densities were too low ($< 1/m^2$) for reliable analysis in the

TABLE 3. PROBABILITIES (CHI P) FOR TREATMENT EFFECTS FOR DEEP STREAM (DS) AND MOUNT BENGER (MB) TURF AND TUSSOCK SAMPLES FOR MAIN INVERTEBRATE TAXA.
Where main effects were not significant, differences for individual dates are shown. 'id' = insufficient data for analyses.

| CLASS | ORDER | DEEP STREAM | | MOUNT BENGER | | TREATMENT DIFFERENCES |
		TURF	TUSSOCK	TURF	TUSSOCK	FOR INDIVIDUAL DATES
Platyhelminthes		0.385	0.411	0.231	0.832	
Annelida	Oligochaeta	<0.001	0.003	0.177	0.217	
Mollusca		0.251	0.555	0.018	0.620	
Arachnida	Total	<0.001	0.01	0.002	0.074	
Arachnida	Araneae	<0.001	0.055	0.012	0.143	
Arachnida	Opiliones	<0.001	0.001	<0.001	<0.001	
Crustacea	Total	<0.001	<0.001	<0.001	0.009	
Crustacea	Amphipoda	<0.001	<0.001	<0.001	0.004	
Crustacea	Isopoda	<0.001	<0.001	0.426	0.803	
Myriapoda	Total	<0.001	0.011	<0.001	0.934	
Myriapoda	Chilopoda	<0.001	0.022	0.046	0.239	
Myriapoda	Diplopoda	0.028	0.418	<0.001	<0.001	
Myriapoda	Symphyla	<0.001	0.022	0.019	0.465	
Insecta	Diplura	id	id	id	id	
Insecta	Protura	0.062	0.745	0.537	0.902	
Insecta	Orthoptera (total)	0.051	<0.001	0.169	0.001	
Insecta	Dermaptera	id	id	<0.001	0.721	
Insecta	Psocoptera	<0.001	0.087	–	–	
Insecta	Hemiptera (total)	0.007	0.044	0.208	0.279	MB turf post-burn < pre-burn
Insecta	Hemiptera (Pseudococcidae)	0.002	0.508	0.027	0.174	DS tussock spring and summer post-burn < pre-burn
Insecta	Hymenoptera	<0.001	0.409	<0.001	0.135	
Insecta	Lepidoptera	0.734	0.05	<0.001	0.012	DS turf spring and summer post-burn < pre-burn
Insecta	Neuroptera	id	id	id	id	
Insecta	Trichoptera	id	id	id	id	
Insecta	Coleoptera (total)	<0.001	0.064	<0.001	0.677	DS tussock spring and summer post-burn < pre-burn
Insecta	Diptera	0.467	0.400	0.032	0.062	DS turf spring and summer post-burn < pre-burn
Insecta	Thysanoptera	<0.001	<0.001	0.029	0.072	
Total invertebrates		0.002	0.175	<0.001	0.244	DS tussock spring and summer post-burn < pre-burn

study area in both turf and tussock samples. Table 4, which is presented at the end of this section, summarises the findings for each invertebrate group reported below.

3.2.1 Deep Stream

Total invertebrate density in control plots remained quite consistent throughout the sampling period for both turf and tussock samples (Fig. 3A & B). The immediate effect of the spring and summer burns in 2001 was to reduce the number of invertebrates to about 8% and 5%, respectively, of pre-burn densities in turf samples (Fig. 3A), and to about 12% and 18% of pre-burn densities in tussock samples (Fig. 3B). The treatment effects were significant for turf samples (Table 3).

Coleoptera densities were less variable between replicate plots than many other taxa, and remained quite consistent in control plots throughout the study period in both turf and tussock samples (Fig. 3C & D). There were significant reductions in density after both burn treatments in turf samples, but not in tussock samples (Table 3). Recovery was evident for the family as a whole within 1 year after the burn.

Annelid densities in control plots varied considerably between dates, but the treatment effects were significant for both turf and tussock samples (Table 3). In both treatments, there was some recovery of annelid numbers during the year following treatment, but they then declined substantially in January 2003. By 2005, the population had recovered to levels similar to the control plots.

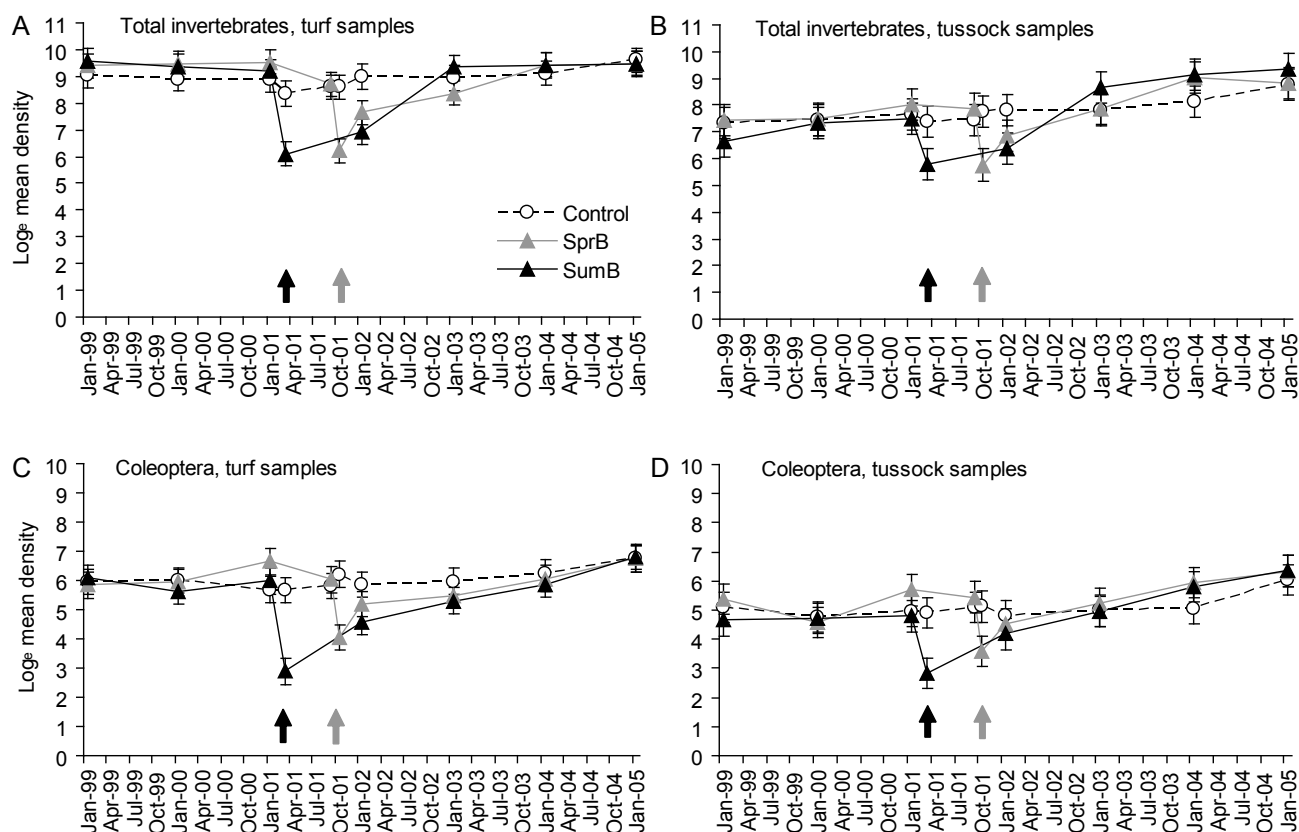Figure 3. Mean density (no. individuals/m^2) of A. total invertebrates in turf; B. total invertebrates in tussock; C. Coleoptera in turf; and D. Coleoptera in tussock at Deep Stream in control, spring-burnt (SprB) and summer-burnt (SumB) plots. Density is expressed as log$_e$ mean density throughout the study period. Error bars represent 2 SEMs. Arrows indicate summer (black arrow) and spring (grey arrow) burn dates.

Arachnid densities were reduced significantly in both turf and tussock samples (Table 3). Burn treatments reduced density in turf samples for Araneae, and in turf and tussock samples for Opiliones. Recovery of the Araneae appeared to be more rapid than for the Opiliones. Opiliones densities became very low in January 2003, but showed signs of recovery in the following years.

Crustacea were represented mainly by Amphipoda and Isopoda. Amphipoda densities were dramatically reduced by the burning treatments in both turf and tussock samples (Table 3). In the spring-burnt plots, there was no evidence of recovery by the 2005 sample date. Control plot densities remained quite consistent over the sampling period. Isopoda were also significantly reduced in density by the burning treatments in turf and tussock samples and, like the Amphipoda, the spring-burnt plot densities remained low to 2005.

Myriapoda were represented by Chilopoda, Diplopoda and Symphyla. Overall, Myriapoda density was reduced significantly in turf and tussock samples at both sites (Table 3), but this reduction was observed mainly during the 2–3 years after the burns. Chilopoda were significantly reduced in density in both turf and tussock samples for all treatments when sampled in 2003 and 2004, but recovery was evident by 2005. Diplopoda densities were very variable between the replicate plots, but there was a significant reduction in density in turf samples immediately post-burn. Symphyla densities declined in turf samples in the 2–3 years post-burn.

Orthoptera were present at low density at DS, although higher densities were observed in the tussock samples than in the turf samples. Densities in turf samples were very variable, but in tussock samples the densities after the spring burn remained very low compared with control plots and pre-burn densities.

Following burning, densities of Psocoptera (detritivores that did not occur at MB) were significantly reduced in the turf samples (Table 3), where their density was initially higher than in tussock. In both turf and tussock samples, densities post-burn remained very low.

Hemiptera densities were dominated by Pseudococcidae. Numbers of individuals in 0.1-m^2 samples ranged from 0 to over 1000, which suggested that these are very aggregated in the field. A significant reduction was found only in post-burn turf samples (Table 3). Mean density was very variable even in control plots, but both spring and summer burns reduced densities to low levels. There was evidence of recovery by January 2003.

Hymenoptera densities were dominated by Formicidae. Densities were very high and consistent in control turf samples for all sample dates, and there was a significant treatment effect (Table 3). Hymenoptera density was lower and more variable in tussock samples, and there were no significant treatment effects.

Lepidoptera, present mainly as larvae in samples, were significantly reduced in density in tussock samples post-burn (Table 3), but populations had recovered by 2003, and appeared to exceed densities in the control plots by 2004. This increase was not significant, but occurred in both turf and tussock samples.

Diptera, present mainly as larvae in the samples, showed no significant treatment effects (Table 3).

Thysanoptera density was dramatically reduced after spring and summer burns in both turf and tussock samples. However, for both vegetation types, the densities in the summer-burnt plots recovered to densities that were substantially higher than those in the control plots. For example, in the summer-burnt plots, pre-burn density (January 2001) in turf samples was approximately 70 individuals/m², which was reduced to less than 1 individual/m² immediately post-burn, but reached about 5000 individuals/m² by January 2003. A similar pattern was observed in tussock samples.

Spring versus summer burn at Deep Stream

The mean density of invertebrates per plot for each January sampling date is shown in Fig. 4. Densities in control plots were consistent from year to year until 2005, when they increased significantly, largely as a result of greatly increased densities of Protura.

For the 3 years pre-burn (1999–2001), there was no significant difference in invertebrate density between plots, although the variability in 2001 was higher than previous years. In January 2002, 3 months after the spring burn and 10 months after the summer burn, the density of invertebrates in both treatments was significantly reduced compared with the control plots. However, compared with means from the same plots in the previous year, invertebrate densities were significantly reduced for only the spring-burnt plots, as the large variability between the summer-burnt plots in 2001 obscured any differences.

By 2003, invertebrate densities in the spring-burnt plots had returned to levels similar to those before treatment, and those in the summer-burnt plots had increased significantly. In 2004, invertebrate densities in both burnt plots significantly exceeded those in control plots, and this was still the case in 2005. This reflects the increased densities of some of the herbivorous taxa (see section 3.3).

Figure 4.   Mean (±SEM) total density (no. individuals/m²) per plot of invertebrates in each treatment from 1999 to 2005 at Deep Stream. Arrow indicates sampling dates between which the burning treatments occurred. SprB = spring-burnt plots; SumB = summer-burnt plots.
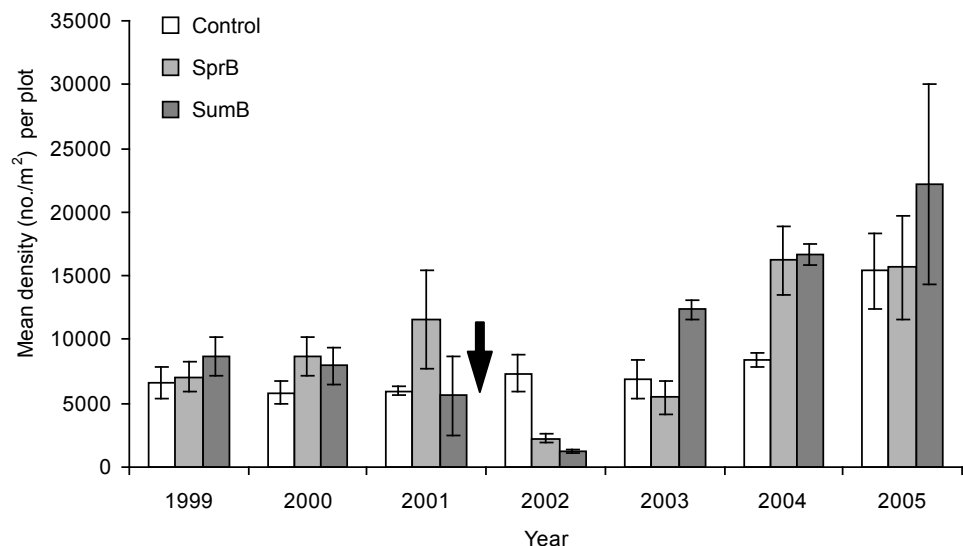
3.2.2 Mount Benger

As for DS, total invertebrate density in control plots at MB remained quite consistent throughout the sampling period for both turf and tussock samples (Fig. 5A & B). The immediate effect of the spring burn in 2000 was less pronounced than at DS, although invertebrate density was still significantly reduced by 40% and 19% of pre-burn densities in 2001 and 2002, respectively.

For total invertebrate density, the generalised linear model showed that there was a significant interaction between treatment and vegetation type. The density of invertebrates (c. 2000 individuals/m^2 before the spring burn) was reduced to about 400 individuals/m^2 in January 2002, just over 1 year after the spring burn (Fig. 5A). No such reduction was observed in the tussock samples (Fig. 5B).

Coleoptera densities were quite consistent between replicate control plots and between dates throughout the study period (Fig. 5C & D). After the spring burn, numbers were reduced significantly in turf samples (Fig. 5C), but there were no significant changes in density in the tussock samples (Fig. 5D).

Annelid density was variable over the study period. There were no significant effects of the spring fire treatment.

Total Arachnida were significantly reduced only in turf samples in January 2002. Araneae densities showed a significant treatment effect only in turf samples (Table 3), but the density of Opiliones was substantially reduced in both turf and tussock samples (Table 3).

A significant treatment effect was found for total Crustacea in turf and tussock samples (Table 3). The fauna was dominated by Amphipoda, which were significantly reduced by the spring burn in both sample types in January 2002; as at DS, there was no evidence of recovery of the population by the end of the study. Isopoda at MB were not significantly affected by the burning treatment, whereas they were at DS.

Total Myriapoda were significantly reduced in density by the spring burn, particularly Diplopoda, which showed no sign of recovery by the end of the study in either turf or tussock samples. Symphyla and Chilopoda showed significant treatment effects in turf samples only (Table 3).

Orthoptera densities were significantly reduced in tussock samples from immediately post-burn to the end of the study period. As at DS, this reduction was mainly attributable to Blattidae densities being reduced to almost zero in tussock samples after the burn.

Hemiptera densities were dominated by Pseudococcidae, as they were at DS. However, at MB the spring burn reduced densities significantly only in turf
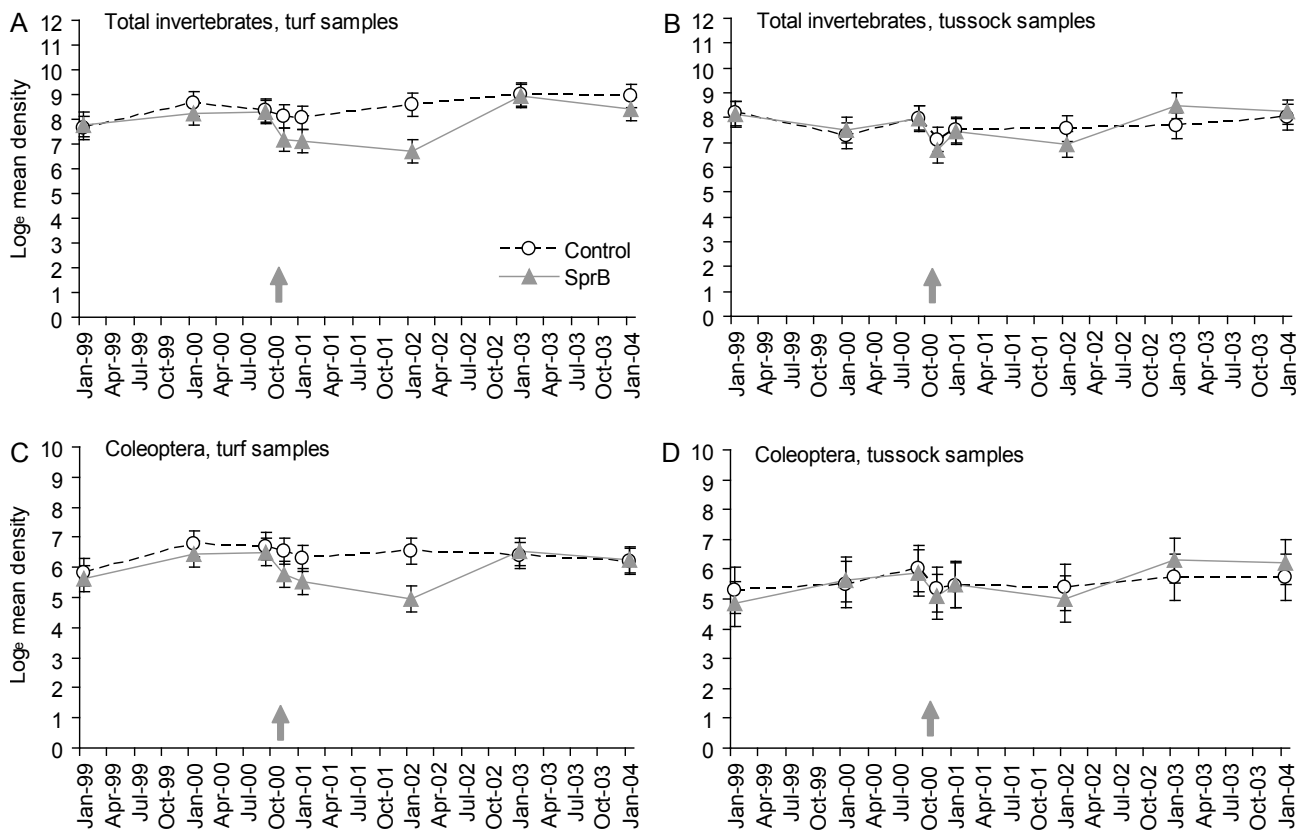
Figure 5.   Mean density (no. individuals/m^2) of A. total invertebrates in turf; B. total invertebrates in tussock; C. Coleoptera in turf; and D. Coleoptera in tussock at Mount Benger in control and spring-burnt (SprB) plots. Density is expressed as log$_e$ mean density throughout the study period. Error bars represent 2 SEMs. The grey arrow indicates the spring burn date.

samples. At this site there was also a large post-burn increase in numbers of Aphididae (not shown) observed in January 2003.

Hymenoptera densities, dominated by Formicidae, were very variable in turf samples, but there was a significant treatment effect (Table 3). Densities were less variable in tussock samples, but there was no significant treatment effect.

Lepidoptera densities were significantly reduced in 2001 after the spring fire in both turf and tussock samples, but populations appeared to have recovered by January 2003.

Thysanoptera densities were significantly reduced only in turf samples (Table 3), but recovered rapidly. In both sample types, densities in January 2003 exceeded pre-burn and control densities, although variability between plots was high.

3.2.3   Summary

The responses of invertebrate taxa found at Deep Stream and Mount Benger to burning treatments are summarised in Table 4.

TABLE 4.   SUMMARY OF RESPONSES OF INVERTEBRATE TAXA TO BURNING TREATMENTS AT DEEP STREAM (DS) AND MOUNT BENGER (MB).

RESPONSE	TAXA	WHERE APPLICABLE
No significant treatment effect	Platyhelminthes	Both sites and sample types
	Protura	Both sites and sample types
	Coleoptera	Both sites tussock
	Pseudococcidae	Both sites tussock
	Hymenoptera	Both sites tussock
	Isopoda	Both sites tussock
	Orthoptera	Both sites turf
	Diptera	DS both sample types
	Mollusca	DS both sample types
	Araneae	MB both sample types
	Annelida	MB both sample types
Density reduced but recovered rapidly	Pseudococcidae	Both sites and sample types
	Coleoptera	Both sites turf
	Diptera	DS
Density reduced but recovered by Jan 2005	Annelida	DS turf
	Isopoda	DS turf
	Chilopoda	DS turf
	Araneae	DS turf
	Symphyla	DS turf
	Lepidoptera	MB
Density reduced and little if any recovery by Jan 2005	Amphipoda	Both sites and sample types
	Psocoptera	DS turf
	Hymenoptera	DS turf
	Orthoptera (Blattidae)	DS spring burn and MB tussock
	Diplopoda	MB
Density reduced but then 'rebounded'	Thysanoptera	DS in particular
	Lepidoptera	DS summer burn
Differences between sites	Annelida	Greater impact DS turf than MB turf
	Myriopoda	Greater impact DS turf than MB turf
	Hemiptera	Faster recovery MB than DS both sample types
	Coleoptera	Greater impact DS than MB both sample types
Differences between vegetation sample types	Myriopoda	Main effects in turf
	Orthoptera (Blattidae)	Main effects in tussock
	Hymenoptera	Main effects in turf

3.3 EFFECT OF BURNING TREATMENTS ON COMMUNITY TROPHIC STRUCTURE

Short-term (2–3 months post-burn) and medium-term (36 months post-burn) changes in the trophic group composition of the invertebrate fauna are discussed below. The trophic structure of the invertebrate communities was similar for the two sites and vegetation types pre-burn (Fig. 6A), with herbivores and detritivores present at similar densities and comprising similar proportions of the invertebrate fauna. Carnivores were slightly less well represented and fungivores comprised a small proportion of the invertebrate fauna. However, as mentioned previously, Collembola, which are primarily fungivores, have not been included in this study.

3.3.1   2–3 months post-burn

Figure 6B suggests that 2–3 months post-burn, densities were reduced for all groups and the proportional structure of the community had changed, particularly at DS.

At DS, the data indicate that the proportion of herbivores in the community was reduced to about 10% of the total, whereas the proportion of detritivores increased to 70% (turf) and 55% (tussock). A comparison of Fig. 6A and 6B suggests that these proportional changes were attributable mainly to the substantial decline in the density of herbivores (mainly Pseudococcidae, Curculionidae and Thysanoptera) and a lesser decline in detritivore densities after burning.

At MB, the community trophic structure was little changed following burning, except that fungivores were almost totally removed (Fig. 6B). This may have mainly been due to reductions in the density of Protura in the spring-burnt plots. Unlike at DS, by the January following the spring burn, the density of Pseudococcidae in the tussock plots at MB had already recovered almost to pre-burn densities.

3.3.2   3 years post-burn

After 3 years, the picture in the burnt plots was even more different from the long-term averages of the control plots, with much greater densities of herbivores, largely resulting from the huge 'rebound' response of Pseudococcidae and other Hemiptera, and Thysanoptera (Fig. 6C). At DS, the increase in the proportion of carnivores in turf samples was a result mainly of the recovery of Araneae (Appendix 4). At MB, the reappearance of fungivores was represented mainly by Protura and Pauropoda (data not presented).

Figure 7 shows the mean densities of invertebrates in the major trophic groups (excluding Hymenoptera) each year for the years preceding and following the spring-burn treatments at DS and MB (Fig. 7A & C); and for the years preceding and following the summer-burn treatment at DS (Fig. 7B). The figure shows that the density of some of the functional groups was quite variable between years before treatments were applied. For example, there were higher densities of detritivores (mainly Annelida, Amphipoda and Diptera larvae) in turf (but not tussock) at MB in January 2000 compared with 1999; conversely, there was a greater density of herbivores in tussock at MB in January 1999 compared with 2000, almost entirely due to a greater density of Pseudococcidae. Generally however, apart from these exceptions, the pre-treatment densities of each of the trophic groups were quite similar.

A   Control

B   2–3 months post-burn

C   36 months post-burn
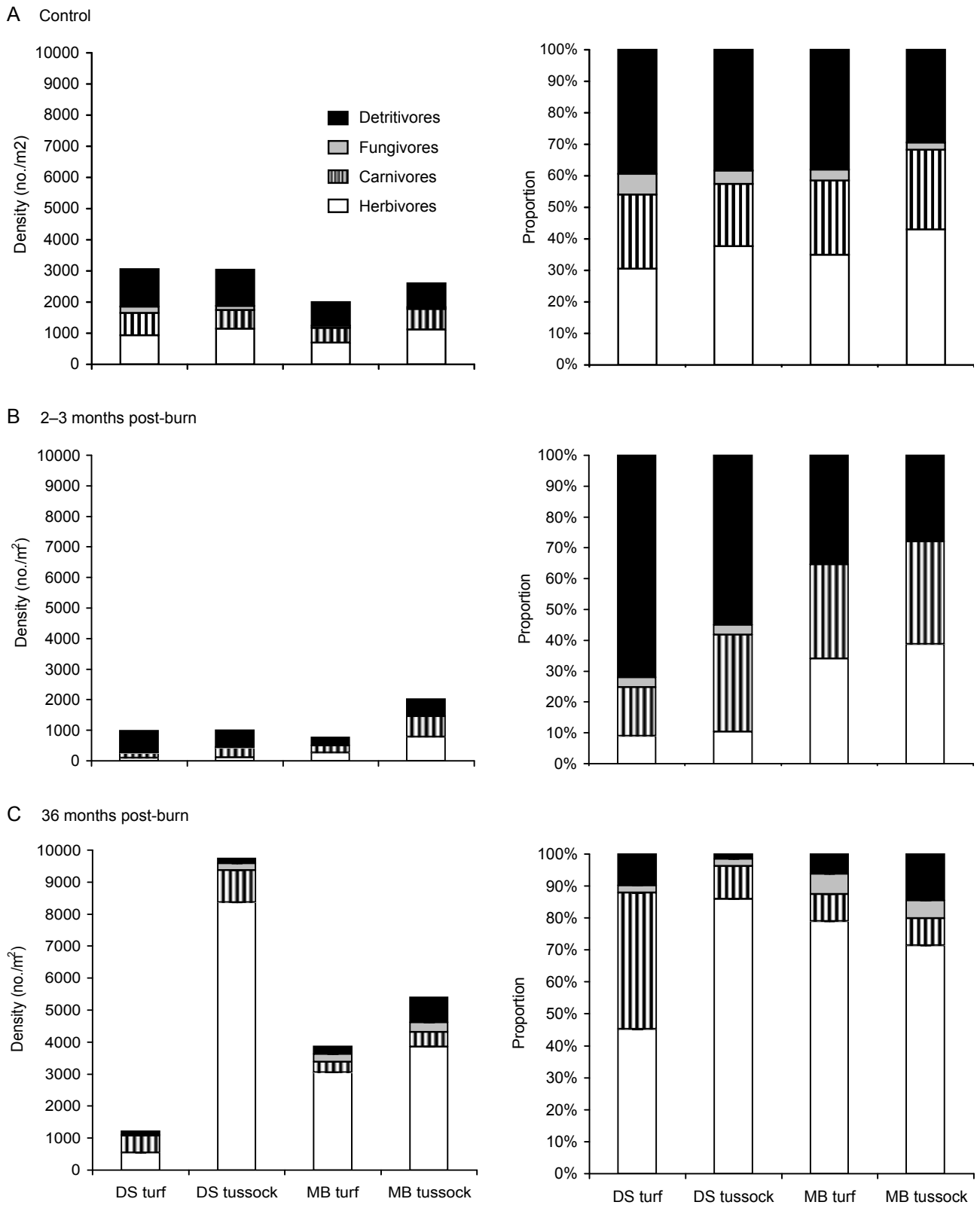
Figure 6.   Mean density (no. individuals/m²) and proportion (%) of invertebrate fauna in each trophic group A. in control plots;
B. 2–3 months post-burn; and C. 36 months post-burn.

Figure 7. Mean density of invertebrates (excluding Hymenoptera) in each trophic group shown for consecutive January samples. A. Deep Stream—spring burn (1999–2005); B. Deep Stream—summer burn (1999–2005); and C. Mount Benger—spring burn (1999–2004). Open bars are pre-burn (all plots) and grey bars are post-burn in consecutive January samples.
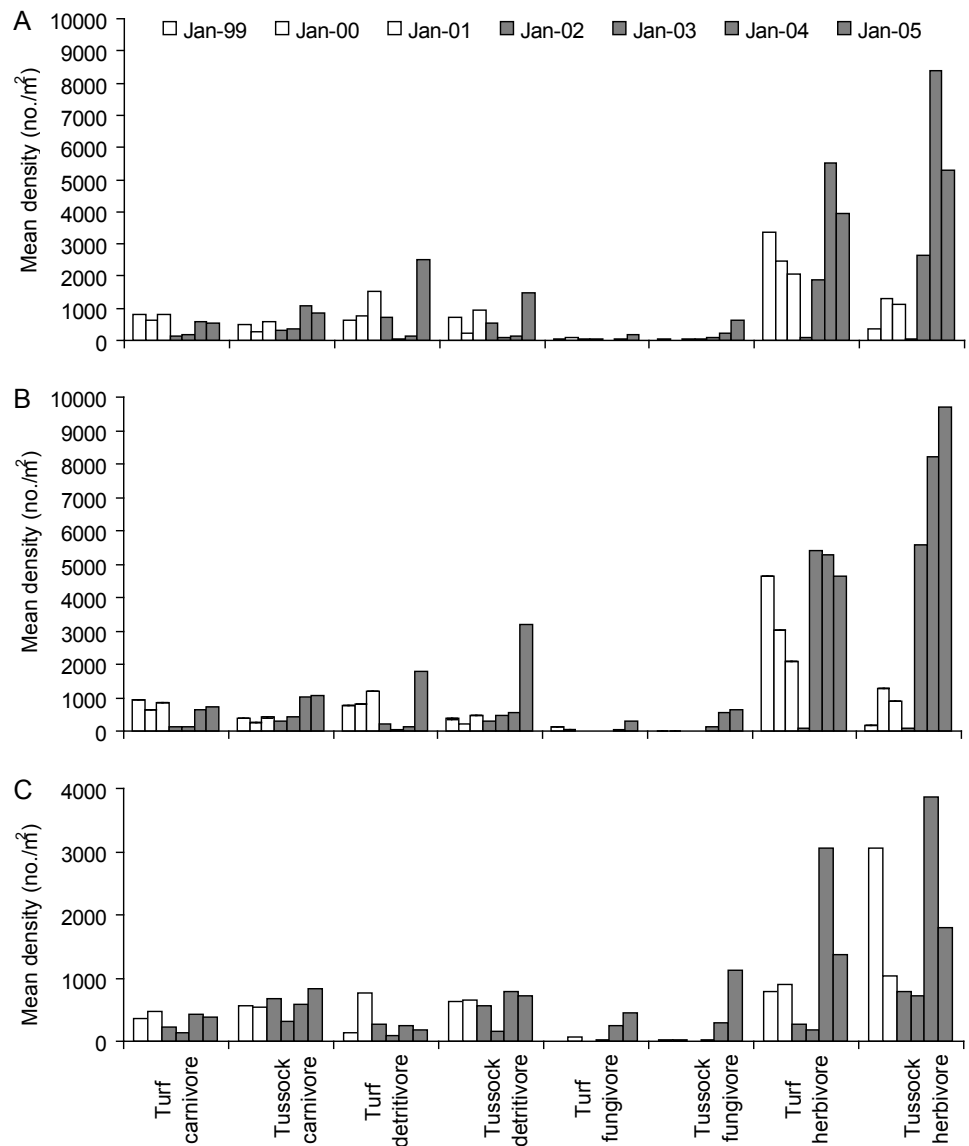
After treatment, herbivores were most severely and immediately reduced in abundance at both sites and vegetation types, but particularly at DS for both spring and summer-burns. However, in the subsequent years, the abundance of herbivores increased and in most cases exceeded pre-burn densities, attributable mainly to Hemiptera (especially Pseudococcidae) and Thysanoptera, as discussed above.

The post-burn response in detritivore density differed between the two sites, particularly for the fourth year. At DS, detritivore densities in turf and tussock samples exceeded pre-burn levels by 2005. In the spring-burnt turf samples, detritivores comprised mainly Diptera larvae, Annelida and Symphyla. However, in the summer-burnt tussock samples, it comprised mainly Annelida and Diplopoda (data not presented). Detritivores exhibited a delayed response to burning, suggesting that environmental change rather than the direct effects of the fire precipitated their decline; e.g. it may have been caused by a reduction in litter, which provides a food source, habitat and insulation from temperature and humidity changes.

The density of fungivores at MB appeared to increase progressively following the spring fire (Fig. 7C). This response also occurred at DS, but less significantly (Fig. 7A). As noted above, this was attributable mainly to Pauropoda and Protura (data not presented).

3.4 COLEOPTERA: A DETAILED STUDY

3.4.1 Density, species composition and effect of burn treatments

The mean density (no. individuals/m^2) of Coleoptera in control plots is shown in Fig. 2. At DS, the mean density for control plots for all sample dates was 221 ± 23 individuals/m^2 in turf samples and 203 ± 34 individuals/m^2 in tussock samples. At MB, the equivalent densities were 325 ± 32 and 344 ± 30 individuals/m^2.

The taxonomic composition of the Coleoptera communities at DS and MB is summarised in Appendix 6. Overall, 24 families of Coleoptera were represented at DS and 28 familes at MB, and in total 111 genera and 202 species were found, excluding larvae. The number of Coleoptera species in each genus and family was similar for both sites, although species richness (excluding larvae) was a little higher at DS (142 species) compared with MB (135 species). If larvae are included, 270 taxa in total were identified. However, since some larvae would also be represented by adults this is certainly an overestimate.

The overlap of species between the two sites was about 40%. Exactly 33% of all species were found only at DS, and slightly fewer (25–29%) were found only at MB (Table 5). To assess the similarity of Coleoptera communities between sites and between plots within sites, non-metric MDS ordinations were carried out for coleopteran data pre-burn and 2–3 month post-burn (Fig. 8A & B). Both MDS ordinations show complete faunal separation between the two sites, suggesting that the coleopteran species abundance patterns were quite different at DS and MB. For the pre-burn data, the replicate plots within sites varied from close faunal similarity (DS control plots) to wide variability (MB spring-burnt plots) (Fig. 8A). For the post-burn data, there is very close faunal similarity between the DS spring- and summer-burnt plots, and the MB spring-burnt plots were also quite closely clustered in comparison with the control plots (Fig. 8B). The stress values (a measure of 'goodness of fit') for the coordinates for both pre- and post-burn MDS ordinations indicated a high level of confidence; it is generally

TABLE 5. SUMMARY OF NUMBER (AND %) OF COLEOPTERA SPECIES AT DEEP STREAM (DS) AND MOUNT BENGER (MB) IN DIFFERENT SAMPLE TYPES.

SITE	SAMPLE	NUMBER OF SPECIES/MORPHOSPECIES (%)			
		INCLUDING LARVAE		EXCLUDING LARVAE	
DS only	Turf only	42	(15.5)	32	(15.8)
	Tussock only	22	(8.2)	17	(8.4)
	Total	89	(33.0)	67	(33.2)
MB only	Turf only	41	(15.2)	34	(16.8)
	Tussock only	17	(6.3)	13	(6.4)
	Total	68	(25.2)	59	(29.2)
Both DS and MB	Turf only	6	(2.2)	5	(2.5)
	Tussock only	1	(0.4)	1	(0.5)
	Total	113	(41.9)	76	(37.6)
Total DS		202	(74.8)	142	(70.3)
Total MB		181	(67.0)	135	(66.8)
Total DS and MB		270		202	

accepted that values below 0.1 suggest an excellent fit, whereas values above 0.15 are unacceptable.

Non-metric MDS ordinations using species presence-absence data also gave complete separation of points for the two sites (Fig. 9). For the pre-burn data, there was a similar degree of spread across plots designated for the treatments at DS, but more clustering of plots at MB (Fig. 9A). Post-burn, the DS plots clustered more closely, especially the spring-burnt plots, suggesting that Coleoptera species composition was more similar after treatment than before (Fig. 9B).

Figure 8. Multidimensional scaling (MDS) ordinations for Coleoptera species density for each of the replicate field plots at each site. A. Pre-burn samples and B. 2–3 months post-burn samples for Deep Stream (DS; circles) and Mount Benger (MB; squares), showing control, spring-burnt (SprB) and summer-burnt (SumB) plots. The closer the points, the more similar are the densities of each species.

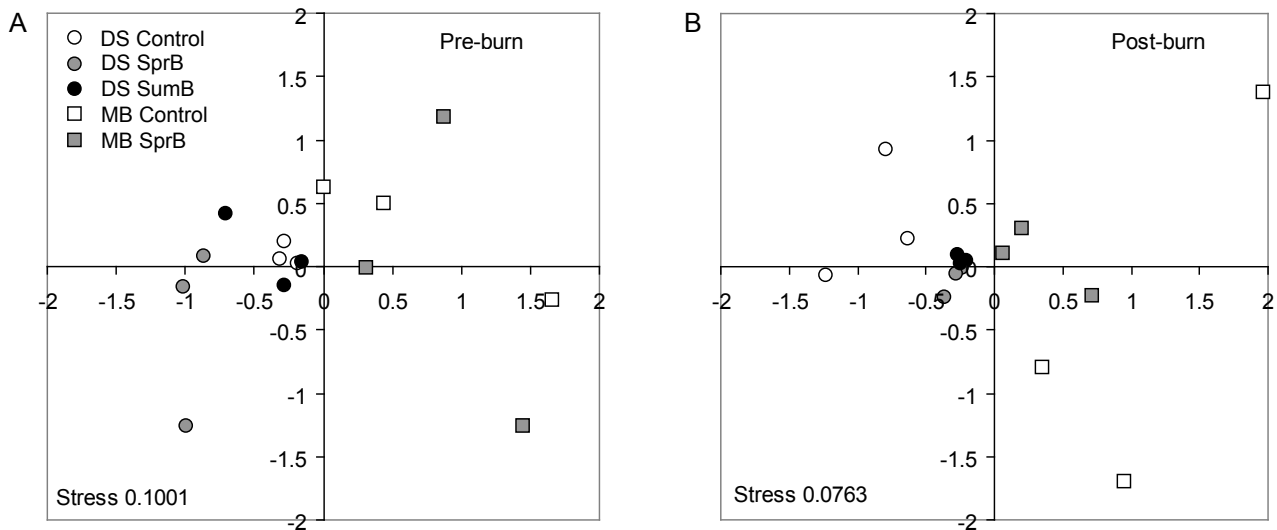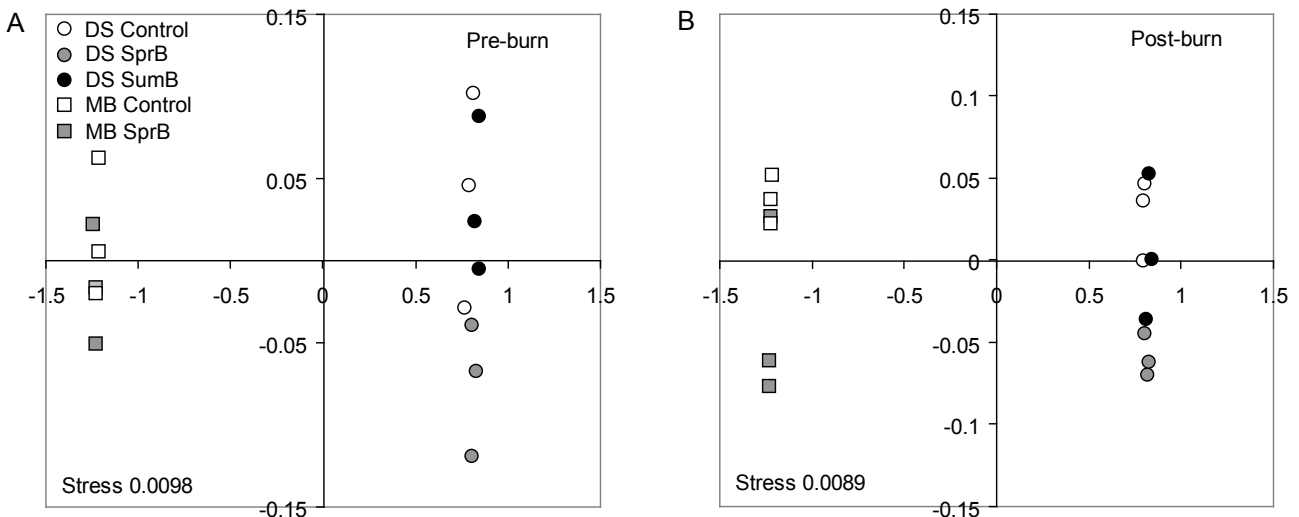Figure 9. Multidimensional scaling (MDS) ordinations for Coleoptera species presence/absence data for each of the replicate field plots at each site. A. Pre-burn samples and B. 2–3 months post-burn samples for Deep Stream (DS; circles) and Mount Benger (MB; squares), showing control, spring-burnt (SprB) and summer-burnt (SumB) plots. The closer the points, the more similar the species composition of each plot.

3.4.2   Species richness

Analysis of species richness data (number of species) for total Coleoptera species (i.e. pooled for all turf plus tussock samples) showed that site and treatment had significant effects on species richness. Over the study period, species richness in control plots at DS and MB was significantly different (Wald statistic = 11.69, df = 1, $P < 0.001$), with means of 51 species and 71 species, respectively (back-transformed $\log_e$ values).

The effect of the burning treatments on species richness is illustrated in Fig. 10, which shows mean species richness $\log_e$-transformed with the back-transformed means (i.e. no. species/m²) superimposed.

For turf samples at DS, there was no significant difference between the control and treatment plots prior to treatment in January 2001, with a range of 31–39 species/m² recorded (Fig. 10A). In January 2002, species richness dropped significantly by about 50% in spring- and summer-burnt plots to a mean of about 15 and 12 species, respectively, while species richness in control plot species richness remained at 33 species. By the following year, species richness in spring- and summer-burnt plots had recovered to 26 and 24 species, respectively, and by January 2004, no significant differences remained between treatments.

Tussock samples at DS (Fig. 10B) are missing data for the control and summer-burnt plots in 2001 (see section 2.4). However, estimates of species richness in control plots were consistent between 2002 and 2003, increasing in 2004. In the spring-burnt plots, a similar pattern was observed in turf and tussock samples, with a reduction from pre-burn species richness in 2002, which then recovered over the following 2 years. The summer-burnt plots followed a very similar pattern to the spring-burnt plots between 2002 and 2004.

For turf samples at MB, estimates of species richness in January 2000 was about 56 species in control plots and 57 species in plots allocated to be burned in spring (Fig. 10A). Two months after the spring burn, mean species richness in the spring-burnt plots was 32 species, and subsequently rose to about 50 species in 2003 and 2004.

Tussock samples at MB followed a similar pattern to turf samples, with an initial reduction in species richness, followed by recovery by January 2003 (Fig. 10B).

Figure 10. Coleoptera species richness in A. turf and B. tussock samples from both sites each year. The histograms show log_e mean number of species ± SEM on the left *y*-axis. The superimposed lines show back-transformed mean numbers of species on the right *y*-axis. Data for 2000 and 2001 are pre-burn for Mount Benger and Deep Stream, respectively. The arrows indicate dates between which the burning treatments were carried out. 2001 data for the burnt tussock treatments at Deep Stream were unavailable.
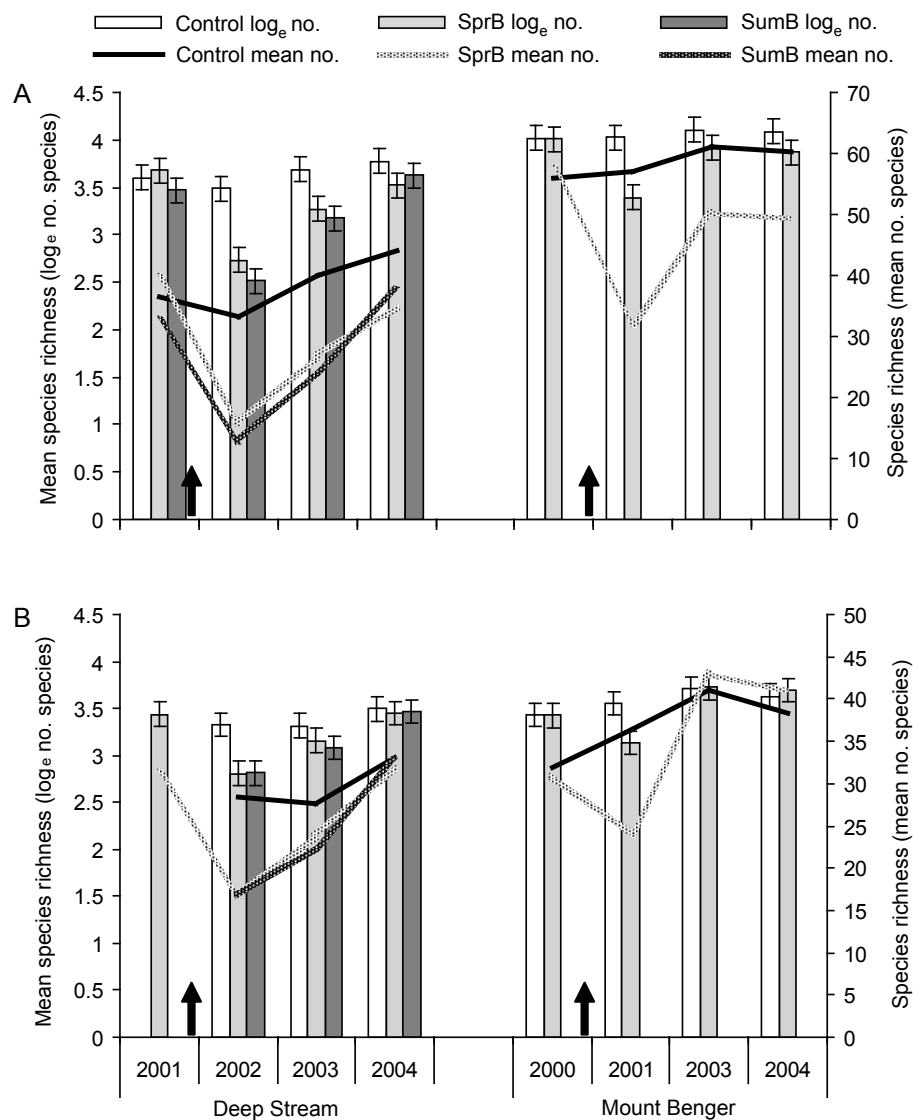
3.4.3   Species diversity

Shannon-Wiener indices of coleopteran species diversity were calculated for each site, sample date, sample type (turf and tussock) and treatment. These data are shown in Fig. 11. The Shannon-Wiener indices calculated for overall species diversity in control plots and combining both vegetation types was significantly higher at MB than DS ($H = 3.245$ and 2.769, respectively; $F = 15.3$, df $= 11.8$, $P < 0.002$).

At DS in January 2001 (pre-treatment), there was no significant difference in the Shannon-Wiener indices between the plots selected for the three treatments as calculated for turf samples (Fig. 11A). For DS control turf samples, there was some variability in species diversity from year to year. However, there was a clear decrease in species diversity in the burnt plots in the January following both the spring and summer fire treatments (January 2002). There was an indication of some recovery in the burnt plots in 2003, and there was no significant difference between the control and burnt plots by 2004.

The index values for the tussock samples from the control plots at DS were consistent between 2002 and 2004, whereas values were significantly lower for the burnt plots in 2002 (Fig. 11B). The Shannon-Wiener indices calculated in subsequent years indicated recovery of species diversity. This recovery was more rapid during 2003–2004 in the summer-burnt tussock samples; index values for the spring-burnt plots remained significantly lower than those of the control plots in 2004 $(F = 15.6$, $df = 2, 8$, $P < 0.05)$, although was not significantly lower than the pre-burn index.

For the turf samples at MB, the Shannon-Wiener indices were a little higher (but more variable) than at DS (Fig. 11A). In January 2000, the mean values for the control and the intended spring-burnt plots were similar, but in 2001 there was a significant reduction in the Shannon-Wiener index for the spring-burnt turf samples. However, by 2003 and 2004 no differences remained between treatments.

The indices for the tussock samples at MB were very similar for both treatments pre-burn in 2000, but reduced significantly in the burnt plots in 2001 and 2003 (Fig. 11B). By 2004, species diversity has recovered to a similar level to that of control plots.

3.4.4   Rank-abundance patterns

The *k*-dominance curves for DS and MB control plots (averaged across years) give an indication of the inherent species diversity at the two sites for turf and tussock (Fig. 12A & B). The lower the curves on the plot, the more diverse are the species assemblages. The *k*-dominance curves indicate that species diversity is generally higher at MB than DS, but this is more pronounced for the turf Coleoptera community than for tussock. This supports the Shannon-Wiener index data (section 3.4.3). Curves for each site, date and sample vegetation type have been plotted in Fig. 13.

For DS spring-burnt plots, the *k*-dominance curves for turf samples indicate that the Coleoptera species assemblage was more diverse in the pre-burn samples taken in 2001 than in any of the post-burn samples (Fig. 13A). For the tussock samples, the curves are less spread and show a similar pattern to each other in successive years (Fig. 13B). For the summer burn treatment, the *k*-dominance curves for turf samples show a similar pattern to the spring burn data, except that the pre-burn and 2004 curves are almost superimposed (Fig. 13C), suggesting that the Coleoptera species assemblage recovered to a greater extent following the summer burn treatment than following the spring burn treatment. The tussock data for summer-burnt plots in 2001 were not available, but the 2002 curve indicates a large reduction in diversity compared with the 2003 and 2004 curves, which were very similar (Fig. 13D).

For MB spring-burnt plots, the *k*-dominance curves for turf samples in 2001 (2 months post-burn) is clearly separated out; however, the 2003 and 2004 curves are very close to the pre-burn curve (Fig. 13E). As at DS, the curves for the tussock samples are less separated between sample dates (Fig. 13F).
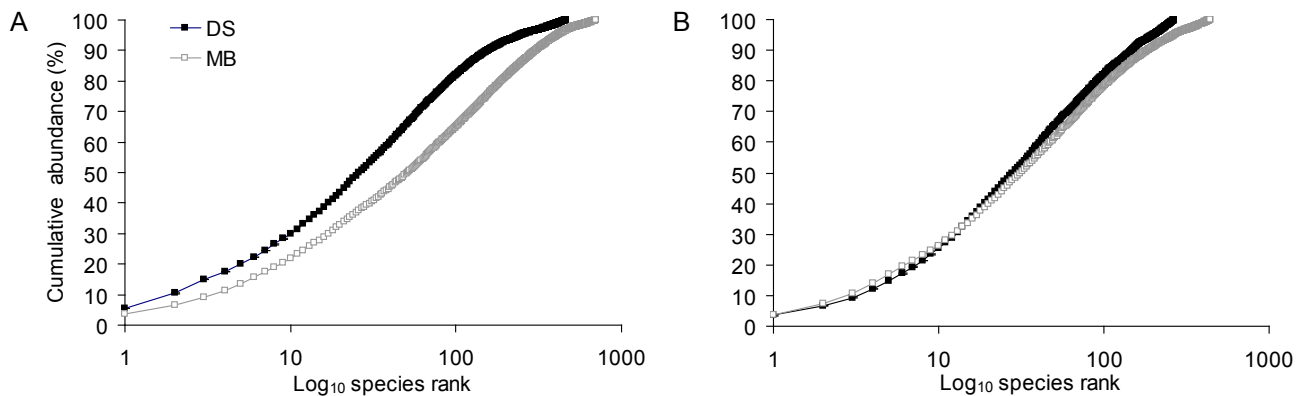
Figure 12.   *k*-dominance curves for Coleoptera at Deep Stream (DS) and Mount Benger (MB) in A. turf and B. tussock samples.
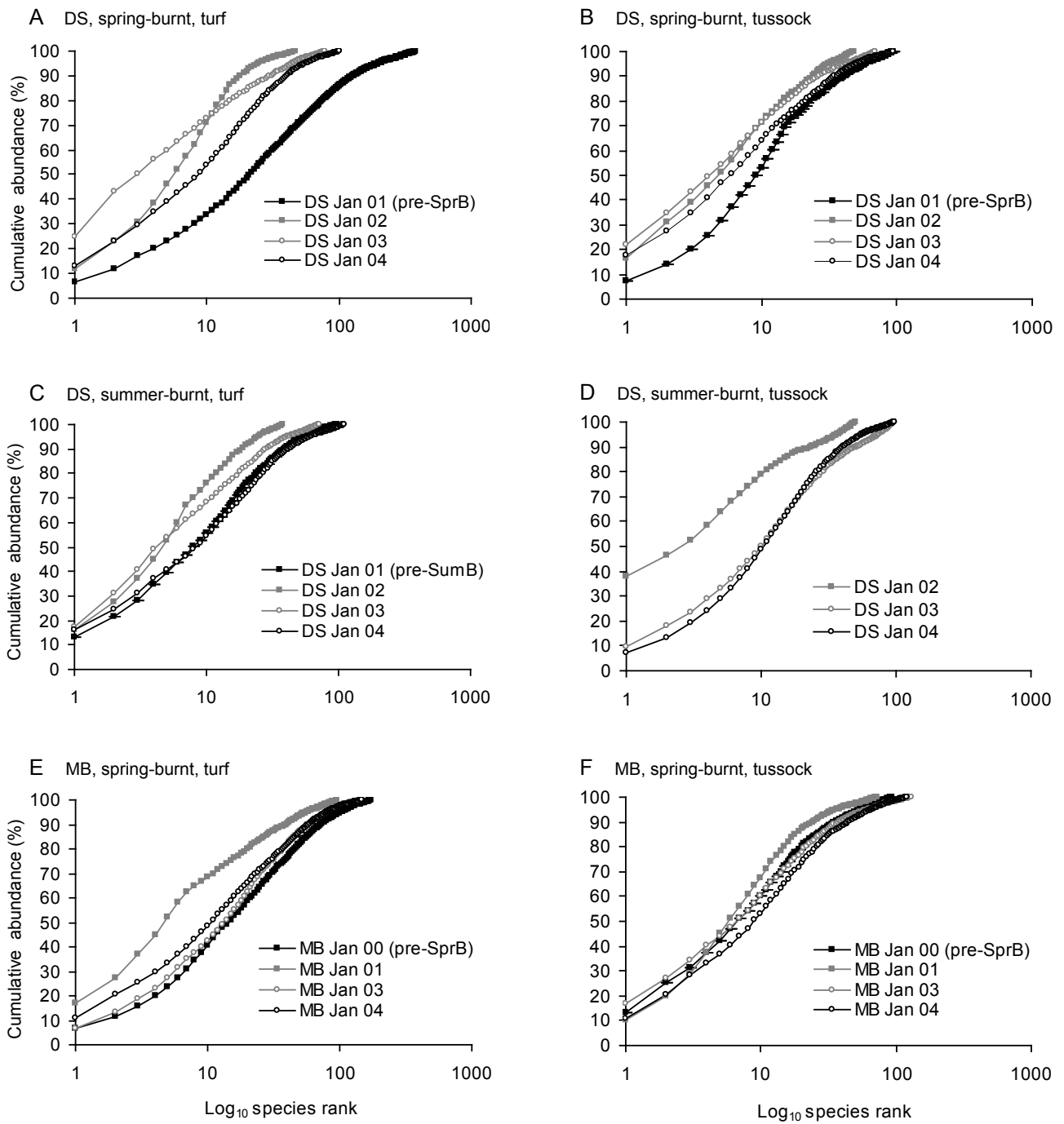
Figure 13. *k*-dominance curves for Coleoptera for each sampling date at Deep Stream (DS) and Mount Benger (MB) pre- and post-burn.
A. Deep Stream spring-burnt plots, turf samples; B. Deep Stream spring-burnt plots, tussock samples; C. Deep Stream summer-burnt plots, turf samples; D. Deep Stream summer-burnt plots, tussock samples; E. Mount Benger spring-burnt plots, turf samples; and F. Mount Benger spring-burnt plots, tussock samples.

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3.4.5 Community trophic structure and response to treatments

The proportion of Coleoptera species and individuals in each trophic group for both sites, all dates and all treatments is shown in Fig. 14. The most noticeable difference between these findings and those reported in section 3.3 for the invertebrate fauna in general is that the Coleoptera were dominated by carnivores (mainly Staphylinidae), comprising 50% or more of all individuals in most cases. In contrast, there was a more even distribution of herbivores, carnivores and detritivores for the total invertebrates, as indicated in Fig. 6A.

The proportion of species in each trophic group appeared to change little between years and burning treatments, except for the initial (2002) decrease in the proportion of herbivore species in turf and tussock samples from spring-burnt plots at DS (Fig. 14). Similarly, there was little difference between treatments in the proportion of Coleoptera individuals in each trophic group. A restricted maximum likelihood analysis of Coleoptera individuals from both sites (turf and tussock treatments combined) showed that control plots had a significantly lower proportion of carnivores (control = 45%; burnt = 65%; $F = 4.87$, df = 2, 10, $P = 0.033$) and a higher proportion of herbivores (control = 47%, burnt = 27%; $F = 6.92$, df = 2, 10, $P = 0.013$). However, since there was no significant treatment × date interaction, these differences were likely to have been present pre-burn, as indicated by Fig. 14.
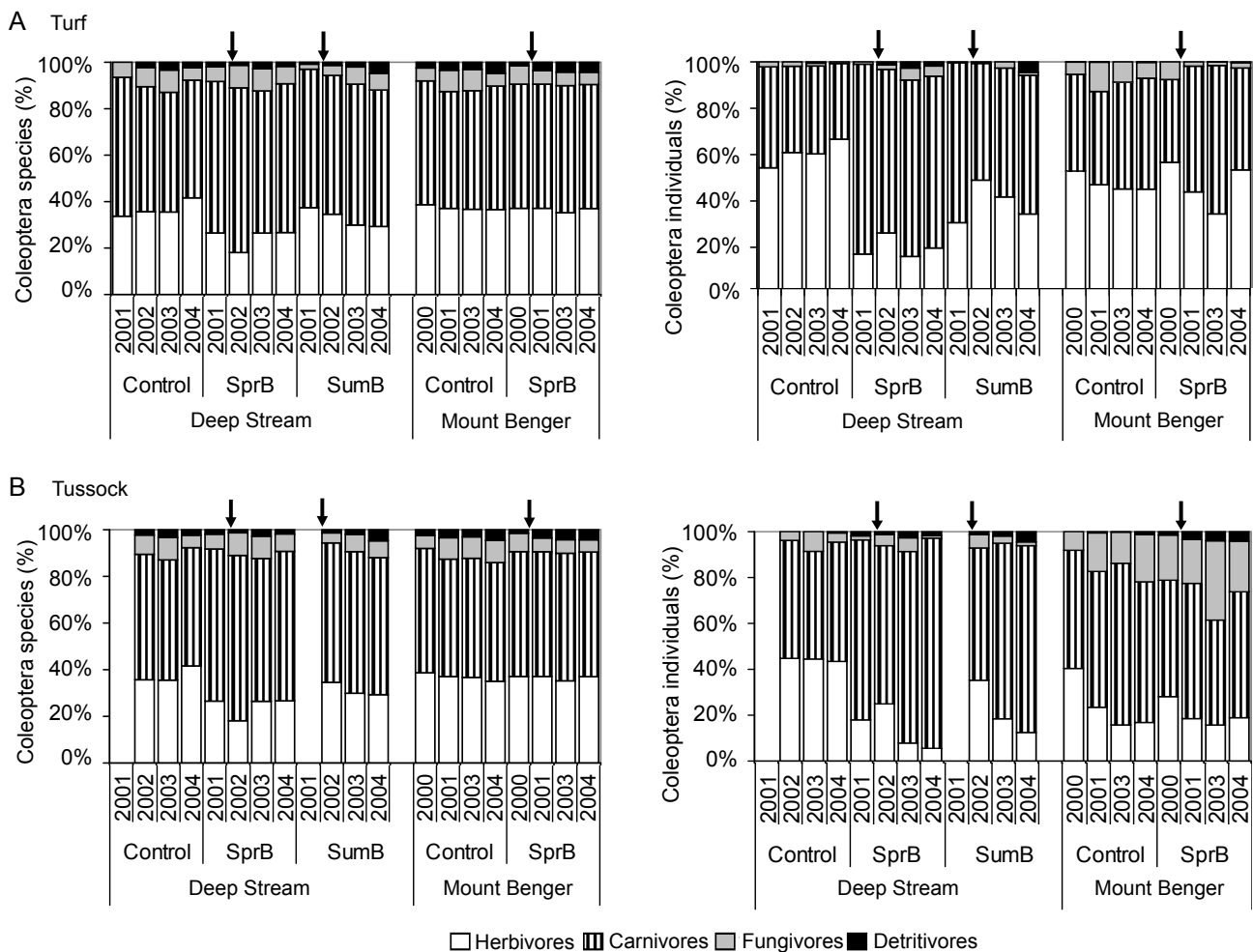
Figure 14. Percentage of Coleoptera species and individuals in each trophic group for each treatment and January sampling date in A. turf and B. tussock samples. The arrows indicate dates between which the burning treatments were carried out. SprB = spring-burnt plots; SumB = summer-burnt plots.

There was a higher proportion of coleopteran fungivores in the MB tussock samples than in the DS tussock samples or the turf samples from both sites (Fig. 14). This group was dominated by the Family Ptiliidae. This family, comprising three species, was present in spring-burnt tussock plots at MB in January 2003 in densities of over 200 individuals/m^2, but was far less abundant in turf samples or DS tussock samples. Reasons for this positive response to burning in spring are unclear. The small proportion of fungivores that were present in MB turf samples (mainly Ptiliidae and Corylophidae) declined to a very low proportion of the fauna after the spring burn treatment.

The proportion of individual herbivores and carnivores in DS turf and tussock samples in control plots was quite consistent between years, with 55–65% of the fauna comprising herbivores and the majority of the balance being carnivores (Fig. 14). The proportions found in the spring-burnt plots, however, were quite different from the control plots, even pre-treatment, with a much greater proportion of carnivores, attributable mainly to by far the most abundant family, the Staphylinidae. For example, in 2001, the mean density of Staphylinidae individuals in control plot turf samples was 43.3 ± 0.33 individuals/m^2, compared with 208.7 ± 1.8 individuals/m^2 in the plots allocated to be burned in spring.

3.4.6   Exotic component of the community

In total, 22 Coleoptera species/morphospecies were classified as exotic (Table 6); five of these were only found at DS, nine at MB, and eight were found at both sites. The proportion of the Coleoptera fauna of exotic origin was 9.2% at DS and 12.6% at MB. Two of the species present were deliberately introduced as biological control agents (Table 6).

At DS, the proportion of species and individuals that were exotic appeared to increase successively between 2001 and 2004 (Fig. 15A & B). However, the proportions increased in both control and burnt plots, suggesting that this was not a treatment effect. At MB, the proportion of exotic species and individuals was generally consistent between years and treatments (Fig. 15A & B).

At both sites, more exotic species were found in turf compared with tussock samples (Table 6), but the mean density of exotic species did not exceed 6 individuals/m^2 in either sample type (Fig. 15C). The generalised linear model found no significant effects of treatment on the proportion of exotic species or individuals present.

TABLE 6.   MAXIMUM DENSITY (NO. INDIVIDUALS/m²) OF EXOTIC COLEOPTERA
SPECIES FOUND AT EACH SITE AND SAMPLE TYPE.

'–' = not present.

FAMILY	SPECIES	DEEP STREAM		MOUNT BENGER	
		TURF	TUSSOCK	TURF	TUSSOCK
Anthribidae	*Euciodes suturalis*	0.5	–	0.5	–
Archeocryptidae	*Archeocrypticus topali*	–	–	0.5	–
Coccinellidae	*Coccinella 11-punctata**	2.0	3.3	0.5	4.4
Coccinellidae	*Coccinella leonina*	0.5	1.1	0.5	–
Cryptophagidae	*Cryptophagus* DS sp. 1	0.5	1.1	–	–
Cryptophagidae	*Cryptophagus* DS sp. 2	–	6.7	0.5	1.1
Curculionidae	*Listronotus bonariensis*	0.5	–	5.5	3.3
Curculionidae	*Otiorhynchus ovatus*	–	–	0.5	–
Curculionidae	*Sitona discoideus*	0.5	–	–	–
Curculionidae	*Trichosirocalus horridus**	–	–	0.5	1.1
Dermestidae	*Anthrenocerus australis*	0.5	–	–	–
Dermestidae	*Reesa vespulae*	0.5	1.1	1.5	–
Latridiidae	*Aridius bifasciatus*	0.5	1.1	–	1.1
Latridiidae	*Cartodere* DS sp. 1	2.0	1.1	–	–
Latridiidae	*Corticaria serrata*	1.0	1.1	0.5	–
Mycetophagidae	*Typhaea sterocorea*	–	–	0.5	1.1
Scolytidae	*Hylastes ater*	–	–	0.5	–
Staphylinidae	*Pselaphophus atriventris*	–	–	–	1.1
Staphylinidae	*Pselaphophus* MB sp. 1	–	–	–	1.1
Staphylinidae	*'Quedius'* DS sp. 1	–	–	0.5	1.1
Staphylinidae	*'Quedius'* MB sp. 1	–	–	2.5	2.2
Staphylinidae	*Tachyporus nitidulus*	0.5	1.1	–	–

*   Deliberate introductions for biological control.

The exotic species that reached highest densities in individual samples at DS were
Cartodere DS sp. 1 (Latridiidae) and *Coccinella 11-punctata* (Coccinellidae) in
turf samples; and *Crytptophagus* DS sp. 2 (Cryptophagidae) and *C. 11-punctata*
in tussock samples. At MB, the exotic species that reached highest densities were
Listronotus bonariensis (Curculionidae) and *'Quedius'* MB sp. 1 (Staphylinidae)
in turf samples; and *C. 11-punctata* and *L. bonariensis* in tussock samples. Of
the herbivores, *L. bonariensis* (Argentine stem weevil) was the most commonly
found, with 11 being collected from a single turf sample at MB in January 2000.
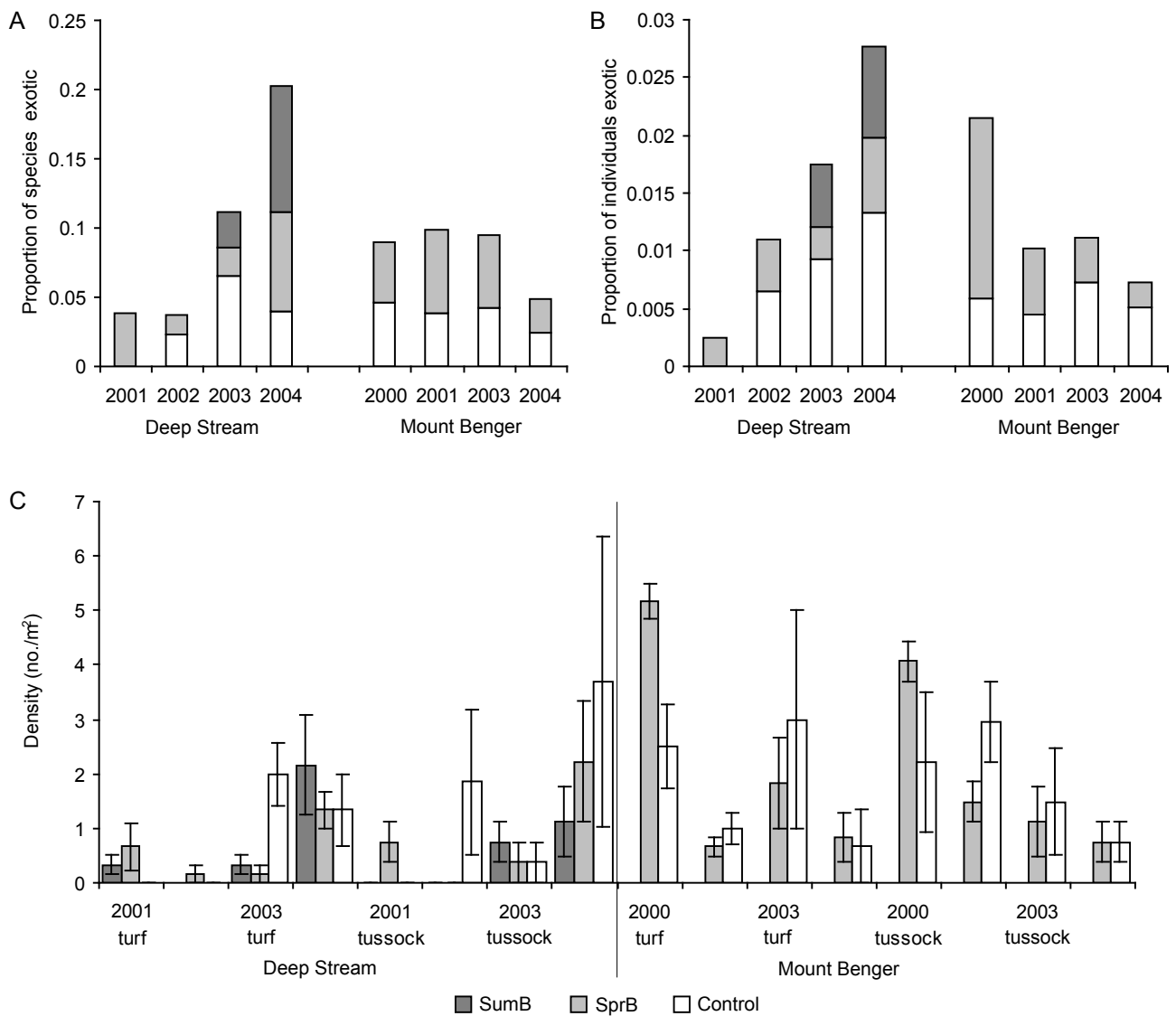
Figure 15. Composition of Coleoptera community for both sites and treatments across all annual January sampling dates. A. Proportion of species that were exotic; B. proportion of individuals that were exotic; and C. mean density of exotic species. SumB = summer-burnt plots; SprB = spring-burnt plots.

4. Discussion

4.1 COMPARISONS BETWEEN DEEP STREAM AND MOUNT BENGER INVERTEBRATE COMMUNITIES

The two sites at DS and MB, which were chosen to represent examples of lower and higher altitude tall tussock grassland, respectively, were both dominated by *Chionochloa rigida*. Soil types are similar, although geological history of the areas is probably quite different, with evidence of glaciation at higher altitudes in the MB area (McEwen 1987). At the time of this study, both areas had been retired from grazing and had not been burned for 10 years or more. DS has a higher average temperature (6.8 °C cf. 4.9ºC) and lower rainfall (993 mm/year cf. 1264 mm/year) than MB (Payton & Pearce 2009).

The composition of the invertebrate communities at these sites has been influenced by combinations of physical and biotic factors. However, our understanding of these relationships is currently insufficiently advanced to be able to explain spatial differences in density and community composition. Previous management history (burning and grazing) for these sites is poorly known further back than 10–20 years, and this will certainly have influenced the invertebrate faunas that we see today.

The total density of the invertebrate fauna (excluding the microarthropods) was considerably higher at DS than at MB, which might be attributable to the higher altitude and cooler average temperature at MB. However, this needs to be considered in the context of the total invertebrate fauna (including microarthropods). Barratt et al. (2006) found that microarthropod (Collembola and Acari) densities in control turf plots at DS and MB averaged over 2001–2003 were 18 579 and 20 413 individuals/m^2, respectively, comprising about 80–90% of the total invertebrate fauna.

4.1.1 Taxonomic composition

At both sites, over 75% of the invertebrate community (in terms of density) comprised Hymenoptera (mainly Formicidae), Myriapoda (mainly Chilopoda), Hemiptera (mainly Pseudococcidae), Crustacea (mainly Amphipoda), Coleoptera (mainly Curculionidae and Staphylinidae beetles) and Arachnida (mainly Araneae). In a previous study, the taxonomic structure of the invertebrate communities at DS and MB were compared with two other tussock grassland sites at Cass (Canterbury) and Tukino (central North Island) (Barratt et al. 2005). Barratt et al. (2005) found that the mean rank of the most abundant taxa (Formicidae (Hymenoptera), Coleoptera and Pseudococcidae (Hemiptera)) were consistent at all sites. These data suggest that, in general, these taxa are amongst the dominant invertebrate components of tussock grassland environments in New Zealand.

The far greater density of Formicidae at DS compared with MB, particularly in turf samples, was one of the most striking differences in the taxonomic composition of the invertebrate fauna between the two sites. Reasons for this are not clear, but it could be the result of altitude-related climatic or biotic variables. Support

for this comes from a study carried out at a higher altitude (about 1600 m a.s.l.) on the Old Man Range (part of the same mountain massif as MB), where ants were found to be very scarce (Scott 2007).

4.1.2   Trophic composition

Despite differences in the density of invertebrates at DS and MB, the trophic structure of the communities at the two sites was quite similar. However, the proportions reported (Fig. 6A) apply only to meso- and macroinvertebrates, and exclude the soil and litter-dwelling microarthropods, such as Collembola and Acari, where fungivores predominate (Barratt et al. 2006). If biomass had been measured, yet another picture would emerge (Saint-Germain et al. 2007). A summary of studies of trophic composition of invertebrates in grassland based on biomass was presented by Curry (1994). Three different studies showed that decomposers comprised 40–96%, herbivores up to 52% and carnivores up to 19%. In general, Curry (1994) found that decomposers (fungivores and detritivores) were the dominant trophic group in grassland, except in very arid environments. These findings are comparable to those from the current study— approximately 42% decomposers (detritivores and fungivores), 35% herbivores and 22% carnivores (Fig. 6A).

4.2   INVERTEBRATE RESPONSES TO BURNING

As expected, most invertebrate groups were initially adversely affected by the burning treatments, with often significant reductions in population density. Some of the groups most severely affected were those dependent upon the litter layer for feeding and for the habitat that it provides. Removal of the litter layer by fire at these sites was reported by Payton & Pearce (2009). The pre-burn above-ground vegetation biomass was similar at DS and MB, at about 27 000–29 000 kg/ha, of which about 60% and 68%, respectively, was litter (Payton & Pearce 2001). The spring burn (November 2000) at MB removed an average of 32% of the above-ground biomass and left much of the ground-cover vegetation intact. However, the spring burn at DS removed 70% of the above-ground biomass, including most of the litter and ground-cover vegetation. This difference was attributed to the lower moisture content of tussock bases and upper soil layers at DS compared with MB (Payton & Pearce 2001). The summer burn at DS caused a similar amount of damage as the spring burn, removing 74% of the above-ground biomass and most of the litter; however, the recovering vegetation was also exposed to winter frosts soon after the burning treatment (Payton 2003).

The Duff Moisture Code (DMC) is one of the Fire Weather Index measurements (Van Wagner 1987) of particular significance to litter-dwelling invertebrates. It is an index of the moisture content of the layer of partially and fully decomposed organic materials lying below the undecomposed litter layer and immediately above the mineral soil. A DMC range of 0–30 denotes minimal to high fire risk. The DMC for the MB spring burn was 6, compared with 14 for the DS spring burn and 26 for the DS summer burn. The greater loss of ground cover at DS following both burns and the higher DMC at DS probably contributed to the more significant impacts of the fires on litter-dwelling invertebrate densities at

DS than at MB. Henig-Sever et al. (2001) found a negative correlation between fire intensity and microarthropod density and community composition. A more intense fire would be expected during summer than spring at DS (and in comparison with the MB spring burn), using plant biomass removal and DMC as indicators; however, it appears that the spring burn at DS was probably more intense than would generally be expected at this time of year.

Table 4 shows that the effects of burning were most prolonged for five taxa and were probably most pronounced for the Amphipoda. These 'land-hoppers' were substantially reduced in density at both sites and vegetation types, and little recovery was observed by January 2005. Terrestrial amphipods are litter dwellers, feeding on decaying organic material and dependent upon a moist, humid habitat. Duncan (1969) found a relationship between litter thickness and amphipod density. Similar burning experiments in Tasmania in button grass vegetation showed a very similar effect, with substantial reductions in density and very slow recovery of Amphipoda (M. Driessen, Department of Primary Industries, Tasmania, pers. comm. 2007). In the current study, the destruction of the litter layer is likely to have caused a collapse in amphipod populations, and it is likely that previous densities would not be restored until the litter layer has had time to re-establish. Psocoptera (at DS) and Diplopoda (at MB) are other litter-feeding invertebrates that also suffered longer-term population density reductions after fire.

Densities of Hymenoptera (mainly ants) declined after burning, particularly in DS turf samples, and densities remained low. In grassland ecosystems that are well adapted to fire, the ant fauna appears to be comparatively resilient to burning. For example, in African savannah, Parr et al. (2004) found that 8 months after a fire there was no significant change in relative ant abundance measured by pitfall trapping; and harvester ants (*Pogonomyrmex rugosus*) appear to be well-adapted to cope with wildfires in the desert grassland of New Mexico, with no measurable change in abundance (Zimmer & Parmenter 1998). It would be expected that in the event of fire, population survival in subterranean nests (to which the highly mobile individuals would most likely retreat) might be quite high. Therefore, the post-burn population density reduction measured in the current study could be attributable to reduced prey and seed availability.

Invertebrate groups that were negatively impacted by fire but recovered by January 2005 were represented mainly in DS turf samples. These included the myriapod orders Symphyla and Chilopoda. The latter are carnivorous, probably feeding on microarthropods such as Collembola and Acari, which were reduced in density after the fire but mostly recovered in the following 2–3 years (Barratt et al. 2006). Post-burn reductions in chilopod densities have also been observed in Illinois prairie (Rice 1932) and in grassland in Spain (Garcia-Ruiz 2001).

Annelid densities were also significantly reduced by fire, but had recovered in DS turf by January 2005. Lumbricidae in tallgrass prairie in Kansas (Callaham Jr. et al. 2003) and prairie in Illinois (Rice 1932) also exhibited declines in density in 0.1-m^2 turf samples after burning. The annelid fauna in this study was dominated by Enchytraeidae. Yeates & Lee (1997) recorded reductions in density of Enchytraeidae in a tussock grassland similar to that reported here 16 months after fire, but the differences were not significant, possibly because of lower sample replication.

Lepidoptera densities at MB were reduced after the spring burn, but recovered to pre-burn and control densities between 2001 and 2003 (Appendix 5). Lepidoptera larvae are either herbivores or litter-feeders, and are probably very susceptible to the high temperatures and acute effects of fire. However, adults are relatively mobile and likely to recolonise quite quickly, especially once plant regrowth occurs and the litter layer re-establishes. In a review of impacts of fire on invertebrates, Warren et al. (1987) found that impacts of fire on Lepidoptera were varied and dependent on habitat and food source, and the way in which these resources were affected by fire (host plant decline, litter removal, etc.).

Invertebrate groups that demonstrated immediate post-burn population impacts followed by rapid recovery were Coleoptera, Pseudococcidae, Diptera and Thysanoptera. Coleoptera will be discussed in more detail below. Declines in pseudococcid (mealybug) densities after burning may have resulted from their generally soft-bodied structure, and hence susceptibility to increased temperature, as well as their immobility and inability to move quickly away from the higher temperatures. However, many mealybugs are found on plant roots in the soil and would have been protected; therefore, other environmental changes following the fires may have resulted in population reduction. Thysanoptera were initially reduced in density but then recovered quite rapidly to achieve densities that were higher than found pre-burn, especially at DS (Table 4). This group is not only very mobile, but has the capacity to increase population density quite quickly.

Changes in invertebrate community structure in the longer term will be influenced by changes in plant species composition. The vegetation in the DS burnt plots became browntop (*Agrostis capillaris* L.) dominant after burning (Payton & Pearce 2001) and native plant species diversity was reduced by about 50% 3 years post-burn (Espie & Barratt 2006).

Substantial loss of litter is likely to delay recovery of litter-dwelling species through altered food and habitat conditions. Loss of tussocks will also potentially reduce biodiversity, since 6–8% of the species at the sites were found only in samples containing *Chionochloa rigida*. The spring burn at DS killed 21–70% of tussock plants (Payton & Pearce 2009).

4.3   SEASONAL EFFECT OF BURNING ON INVERTEBRATES

In general, seasonality of the burning treatments, which could only be compared at DS, did not appear to be a major factor influencing the immediate and longer-term recovery of most invertebrate groups. Irrespective of season, the immediate impact of fire on invertebrate faunas depends upon the intensity and duration of the fire (Curry 1994). At DS, the spring burn was more intense than would be expected, since both spring and summer burns removed much of the litter (Payton & Pearce 2009). Other factors that are likely to result in seasonal difference in invertebrate responses to fire include seasonal diapause, presence of different stages of the life cycle (e.g. surface-dwelling cf. soil-dwelling stages) and differential removal of vegetation (Swengel 2001).

4.4 EFFECT OF BURNING TREATMENTS ON COMMUNITY TROPHIC STRUCTURE

It is well recognised that management practices such as grazing, burning, etc. that change the composition of the sward will inevitably change invertebrate species composition in grassland (Curry 1987). Change in botanical composition can potentially have the most profound effects on monophagous herbivore species (those that eat only one species of plant). However, herbivores in general are dependent upon the standing crop of vegetation, which was severely depleted in the first few months after the fire (NZ Fire Research 2001). The changes that occurred in invertebrate abundance 2–3 months after burning are likely to have been responses to the changed environment of reduced litter and drier soil surface conditions. After 3 years, however, botanical changes had probably influenced the community structure. A discussion of trophic structure and changes brought about by a disturbance such as burning can at best be superficial without data on biomass and energy flow (which was beyond the scope of this study). Nevertheless, our speculative interpretations of some of the major responses seen are discussed in the following sections.

4.4.1 Herbivore response

The massive reduction in herbivore densities 2–3 months after treatment (Fig. 7), especially at DS, probably resulted from the direct effect of the fire causing mortality of invertebrates, as well as indirect effects as a result of the large reduction in available plant material. The relationship between plant biomass and invertebrate biomass was demonstrated by Andrzejewska (1979a). From data collected in Polish grasslands, he calculated that for every 1000 kg DM (dry matter)/ha there is an increase of 20 kg DM/ha of invertebrates. While this clearly cannot be directly applied to New Zealand tussock grassland, especially since invertebrate biomass data are not available for our sites, it could be indicative of the scale of invertebrate biomass loss that might accompany the large plant biomass losses of approximately 13 600 and 25 500 kg DM/ha that were calculated after the spring burns at MB and DS, respectively (Payton & Pearce 2009).

The 'rebound' in herbivore densities measured for Thysanoptera and Lepidoptera (Table 4) following an initial dramatic decline was almost certainly related to the flush of vegetation regrowth. A study carried out close to the MB site showed that 1.5 years after a tussock fire, the level of phosphorus in burnt plots was twice the value of that in control plots, and 2 years after the fire, higher concentrations of nitrogen and phosphorus were available to plants (Ross et al. 2001). In addition, the level of total nitrogen and phosphorus in *Chionochloa rigida* leaves was significantly higher in burnt plots than control plots after 2 years. These increased nutrient levels would contribute to improved plant growth and the nutrient value of vegetation for herbivorous invertebrates.

4.4.2 Carnivore response

Although there was a reduction in carnivore densities in the 1–2 years after spring burning, especially at DS in turf samples (Fig. 7), the response was not large. This perhaps reflects the ability of carnivores to switch to alternative prey items when there are fluctuations in density of the other trophic groups. There was no evidence of a 'rebound' in numbers as the carnivore populations recovered.

4.4.3 Detritivore response

At MB, there was no evidence of a reduction in detritivore densities following burning. However, at DS there was a pronounced decline and then 'rebound' in detritivore densities in both turf and tussock samples after the spring burn, and in tussock samples after the spring and summer burns (Fig. 7). The initial decline could have resulted from reduced litter and more variable temperatures and humidity. The increase in January 2005, however, is more difficult to interpret. Andrzejewska (1979b) emphasised the importance of herbivore faeces as a highly nutritious substrate for saprophagous feeders (here called detritivores), affecting the fecundity of this group. It is conceivable, therefore, that the large increase in herbivore density recorded in January 2004 and 2005 in particular provided the mechanism for the recovery; indeed the observed 'rebound' was mirrored by herbivore densities, despite the herbivores largely comprising Thysanoptera and Pseudococcidae.

4.4.4 Fungivore response

Fungivore densities were very low at both sites and vegetation types (Fig. 7). This is somewhat misleading, since microarthropods, which were not included in this investigation, contribute a large component of the fungivore fauna. However, the 'rebound' of fungivore densities at MB, especially in tussock samples, might be explained by their response to a possible flush of fungal activity on dead organic material and litter that had begun to accumulate in the system after being removed by fire. This effect was far less pronounced at DS, where litter removal by the spring and summer burns was more complete.

4.5 COLEOPTERA: A DETAILED STUDY

Coleoptera were identified to species/morphospecies in this study with an endeavour to include larval stages. However, this presented some major challenges. In all cases, identification to family at least was attempted for larvae. Inevitably, there will have been some errors in our taxonomy for immature stages, which it may be possible to correct in the future, since all specimens have been retained in storage. Taxonomic assignment was particularly demanding for Staphylinidae in the subfamily Aleocharinae, where several species were distinguished as adults but species-level diagnostic characters could not readily be assigned to larvae with the available resources. This subfamily would lend itself well to a molecular approach to linking larvae with adults.

The coleopteran families with the highest recorded number of species were the Curculionidae and Staphylinidae at both sites. This was also found to be the case at 1600 m a.s.l. on the Old Man Range, close to MB (Scott 2007).

The pre-treatment MDS ordination data (Fig. 8A) illustrated the variability in density of individual species between the treatment replicates, varying from close agreement in DS control plots to widely variable in MB plots designated to be burned in spring. This illustrates the heterogenous nature of the Coleoptera population densities at the sites.

4.5.1 Effect of treatments on species richness

Pre-treatment Coleoptera species richness was higher at MB than at DS, and in both cases was higher in turf than tussock samples, possibly as a result of greater plant species diversity in turf samples. Burning reduced coleopteran species richness substantially in turf samples, especially at DS, where it did not recover to pre-burn levels until 2004 for both spring and summer burn treatments. A similar pattern was observed for tussock samples. The similarity of impact for the spring and summer burn treatments probably resulted from the similarity of intensity of the two fires. Both fires removed much of the ground cover layer of plants and the litter layer (Payton & Pearce 2009), reducing food resources for herbivorous families such as Curculionidae, and shelter for many litter-dwelling families such as the Staphylinidae. Furthermore, the spring burn at DS was followed by a period of dry weather (Payton & Pearce 2009), which would have further reduced survival of litter-dwelling species. Conditions following the spring burn at MB were more favourable to Coleoptera species survival, as snow covered the sites a few days after treatment (Payton & Pearce 2009), which would have buffered communities against frost, from which they would have found difficulty in sheltering, and against dehydration.

Fadda et al. (2007) found that species richness of Coleoptera was higher in disturbed sites than undisturbed steppe in southern France because the vegetation contained more early colonising plant species, which supplied vegetation of a higher nutritive value to herbivores and a more diverse supply of prey items for carnivores. They argued that cultivation created soil conditions that were beneficial for Coleoptera with soil-dwelling stages. Although disturbance by burning is unlikely to alter the soil environment substantially, it is known to produce a 'flush' of vegetative regrowth as a result of increased levels of phosphorus and nitrogen available to plants after fire (Ross et al. 2001), which is likely to be beneficial to herbivorous invertebrates.

In a semi-arid shortgrass steppe in New Mexico, USA, Ford (2007) recovered 29 families of Coleoptera (by pitfall trapping) and identified 115 species. Ford (2007) investigated the effect of burning on Coleoptera by comparing 2-ha plots burned in spring with plots burned in summer and unburnt plots. Coleoptera species 'abundance' was not significantly changed 1 year after burning, but species richness significantly increased in the spring-burnt plots; the summer fire treatment had no effect on species richness. This contrasts with our data, where Coleoptera species richness declined significantly at both sites and after both treatments. However, the sampling method used by Ford (2007) might have influenced the results in his study: pitfall traps are a better measure of activity than abundance, and burnt plots with less vegetation and litter might have allowed increased activity of Coleoptera.

4.5.2 Species diversity and rank abundance patterns

The Shannon-Wiener species diversity indices calculated were found to mirror to some extent the decline in Coleoptera species richness and density. This might be expected, since the Shannon-Wiener index takes account of both these variables. However, k-dominance curves for the coleopteran community under different treatments encompass species richness and evenness of spread of individuals between species (Platt et al. 1984). If the k-dominance curves intersect (e.g. as seen for the curves for January 2002 and January 2003 DS spring-burnt turf samples in Fig. 13A), this suggests that the Coleoptera species assemblages are not comparable in terms of intrinsic diversity and that Shannon-Wiener is not necessarily reliable (Platt et al. 1984). Furthermore, the difference in the shape (steepness) of the curves for the pre-spring-burn treatment in the two vegetation types at DS suggests that the evenness of spread of individuals between species is greater for the turf samples than the tussock samples.

If the Shannon-Wiener plots (Fig. 11) are compared with the k-dominance curves for DS spring- and summer-burnt plots for turf samples (Fig. 13A & C), then both indicate a substantial reduction in species diversity in 2002 (3 months post-burn), and to a lesser extent in 2003 (1 year later). However, the Shannon-Wiener indices for 2004 have returned to pre-burn values for both treatments, whereas the k-dominance curve remained distinctly separated, at least for the spring-burnt plots.

For the DS tussock samples, the pattern suggested by the k-dominance curves closely reflects the Shannon-Wiener index values, with diversity decreasing from 2002 to 2003, then returning further towards the pre-burn values by 2004. The summer burn tussock k-dominance curves (Fig. 13D) indicate a large reduction in diversity in 2002 (as do the Shannon-Wiener indices, although the pre-burn values are not available). For the following years, a substantial increase in diversity is indicated by both methods.

For MB, there was generally good agreement between the two methods of species diversity assessment. Apart from a clear separation of the k-dominance curves for 2001 turf samples (Fig. 13E) and significant reduction in Shannon-Wiener values, there is little difference in the following years. The tussock data also suggest little difference in Coleoptera species assemblages (Fig. 13F).

With the exception of a single inconsistency noted above, the Shannon-Wiener and k-dominance approaches give consistent findings, providing a reasonable degree of confidence in the comparative assessment of spring and summer burning treatments on Coleoptera species diversity.

4.5.3 Trophic structure and response to treatments

The trophic structure in the Coleoptera community observed in our study was similar to that found by Fadda et al. (2007) in steppe grassland in southern France, with herbivores comprising about 35% of species in both studies, carnivores about 50% (cf. 30% in France) and the remaining 15% fungivores, detritivores and coprophagous species (cf. 35% in France).

Burning brought about few changes in the trophic structure of the coleopteran community, either in proportion of species or individuals (Fig. 14). However, the analysis of these data did highlight the differences in the proportions of

herbivores and carnivores that occurred between the DS plots before the spring burns took place, particularly with regard to the dominance of carnivores. The effect of burning was, however, evident in MB tussock samples, where the proportion of fungivores increased in 2003, 2 years after treatment.

4.5.4 Exotic component of the community

A large number of exotic organisms have become established in New Zealand, and some represent a threat to native ecosystems. In a recent international review of literature, it was found that about 20% of all exotic insects accidentally or deliberately introduced into semi-natural or natural ecosystems are Coleoptera (C.B. Phillips, AgResearch, unpubl. data 2008).

Exotic Coleoptera have become established in the relatively undisturbed tussock grassland environments at both DS and MB, although at both sites the proportion of exotic species (and individuals) was low. There was no significant or consistent effect from the burning treatments at the two sites. While it might be expected that disturbance by burning would lead to an increase in the exotic component of the fauna, especially if the diversity and abundance of exotic plants increases, the time scale of this study was probably too short to measure such changes. There is very little, if any, comparable data from New Zealand with which to compare these findings.

4.6 LIMITATIONS OF THIS STUDY

The delay in carrying out the MB summer burn treatment reduced the potential for a robust analysis of the effect of season (spring or summer) on the impact of fire and recovery of invertebrate populations and community structure. However, annual sampling of all plots has continued, so further analysis will be possible in the future. Similarly, the discontinuation of processing samples after 2005 has limited our ability in this report to discuss recovery of some taxa that had not returned to pre-burn population densities. Furthermore, the absence of invertebrate data from the DS January 2001 tussock control and summer-burnt plots has limited our ability to fully analyse these data, but again this could be addressed in the future. Finally, it must be remembered that the treated plots were 1 ha in size, and so recolonisation from the surrounding unburnt vegetation is likely to have occurred more rapidly that it would from a large-scale burning programme or from a wild fire. This recolonisation is also likely to occur differentially amongst invertebrates, depending upon their relative mobility.

5. Conclusions

This research has provided data on invertebrate density and trophic structure using two case studies in Otago tussock grassland. For Coleoptera, it was possible to make additional measurements of species richness and diversity, trophic structure and the exotic component.

Since the study reported here was limited by a lack of site replication, the DS and MB sites need to be considered as case studies, limiting the ability to extrapolate the findings to other sites. The study was also limited by the relatively short time scale for post-burn analysis of impacts. However, where clear and substantial short- to medium-term effects have been observed at both sites, it is probably reasonable to cautiously generalise about effects.

The data obtained for Coleoptera in this study are probably the most informative for assessing the impacts of fire on biodiversity, assuming that Coleoptera are a good surrogate for the invertebrate fauna. These data indicate that species richness was initially substantially reduced, but that this returned to pre-burn levels 2–3 years post-burn at both sites and treatments, and the exotic component of the fauna did not change at these sites in the time frame of the study. Species diversity, measured by the Shannon-Wiener index and also presented as k-dominance plots, returned to pre-burn levels within the study period, with the possible exception of the spring-burnt turf samples at DS, as indicated (quite strongly) by the k-dominance curves.

The rest of the invertebrate fauna was not analysed at the species level, and there were no indications that entire groups were removed by the fire treatments. However, there were clear and sometimes severe impacts on elements of the fauna, some of which did not return to pre-burn status within the study period, a case in point being the Amphipoda. Given that Coleoptera was not one of the most severely impacted groups, the impacts on the rest of the fauna need to be considered. As other higher taxa are further analysed at species level, it will be valuable to include these in an analysis of the impact of fire on species richness and diversity.

The comparison of the impact of spring and summer fires on the invertebrate fauna indicated that there were no major differences, at the level of detail possible in this investigation, either for the full range of taxa or for Coleoptera species. Similarly, there were no substantial differences between seasons in the effect on any of the trophic groups within the community. It is unfortunate that the MB summer burn data were not available for analysis in this report, so that the comparison was restricted to a single site. An analysis of individual species in the future might unearth differential effects on taxa of the timing of burning treatments.

6. Recommendations

The authors make the following recommendations, including topics for further research:

- Continue annual sampling and storage of specimens for at least another 5 years to develop a resource of collected material. This has been carried out for 2007, 2008 and 2009. This will allow for longer term effects of burning to be analysed at some stage in the future.

- Store one complete set of unsorted material from both sites (e.g. January 2008 sample) in deep freeze to preserve DNA for future study. This would allow DNA extraction to be carried out for taxa where molecular methods are required to solve taxonomic or systematic problems. Improve standard of curation of remaining collected material to museum standard.

- Integrate invertebrate and plant data, and work towards using data on fire characteristics, and effects on the flora and invertebrates to develop a predictive model that can be tested.

- Encourage students to make use of the material and the data to add value to the information reported so far. Such studies could include:

  —Estimation of treatment impacts on biomass of invertebrate taxa and trophic groups, which is often considered more ecologically meaningful than density.

  —Determination of consequences to native flora of post-burn outbreaks of Pseudococcidae, Thysanoptera and Homoptera, as found in the current study, and the potential for these taxa to transmit plant pathogens.

  —Molecular studies to match larvae with adult stages. This may be limited by the quality of DNA that can be extracted for longer-term alcohol-stored specimens unless stored in deep freeze. This would be particularly valuable for species-rich groups such as Staphylinidae, where morphology is particularly challenging.

  —Testing of consistent results from these case study sites to determine whether they apply more universally.

7. Acknowledgements

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Appendix 1

TAXONOMIC GROUPS AND COMMON NAMES OF INVERTEBRATES IDENTIFIED

PHYLUM	SUBPHYLUM	CLASS	ORDER	FAMILY	COMMON NAME
Platyhelminthes		Turbellaria			Flatworms
Annelida		Oligochaeta	Clitellata		Earthworms, potworms
Mollusca		Gastropoda	Pulmonata		Slugs
Mollusca		Gastropoda	Pulmonata		Snails
Arthropoda	Chelicerata	Arachnida	Araneae		Spiders
Arthropoda	Chelicerata	Arachnida	Opiliones		Harvestmen
Arthropoda	Chelicerata	Arachnida	Pseudoscorpionida		Pseudoscorpions
Arthropoda	Crustacea	Malacostraca	Amphipoda		Bush hoppers
Arthropoda	Crustacea	Malacostraca	Isopoda		Woodlice/slaters
Arthropoda	Myriapoda	Chilopoda			Centipedes
Arthropoda	Myriapoda	Diplopoda			Millipedes
Arthropoda	Myriapoda	Symphyla			
Arthropoda	Myriapoda	Pauropoda			
Arthropoda	Hexapoda		Diplura		
Arthropoda	Hexapoda	Entognatha	Protura		
Arthropoda	Hexapoda	Insecta	Orthoptera	Blattidae	Cockroaches
Arthropoda	Hexapoda	Insecta	Orthoptera	Stenopelmatidae	Weta
Arthropoda	Hexapoda	Insecta	Orthoptera	Acrididae	Grasshoppers
Arthropoda	Hexapoda	Insecta	Orthoptera	Gryllidae	Crickets
Arthropoda	Hexapoda	Insecta	Dermaptera		Earwigs
Arthropoda	Hexapoda	Insecta	Psocoptera		Book-lice
Arthropoda	Hexapoda	Insecta	Hemiptera	Homoptera	Aphids and others
Arthropoda	Hexapoda	Insecta	Hemiptera	Pseudococcidae	Mealybugs
Arthropoda	Hexapoda	Insecta	Hemiptera	Heteroptera	True bugs
Arthropoda	Hexapoda	Insecta	Hymenoptera	Formicidae	Ants
Arthropoda	Hexapoda	Insecta	Hymenoptera	Other Hymenoptera	Bees, wasps
Arthropoda	Hexapoda	Insecta	Lepidoptera		Butterflies, moths
Arthropoda	Hexapoda	Insecta	Neuroptera		Lacewings
Arthropoda	Hexapoda	Insecta	Trichoptera		Caddis flies
Arthropoda	Hexapoda	Insecta	Coleoptera	Anthicidae	Ant beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Anthribidae	Fungus weevils
Arthropoda	Hexapoda	Insecta	Coleoptera	Byrrhidae	Moss beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Carabidae	Ground beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Cerambycidae	Longhorn beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Chrysomelidae	Leaf beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Coccinellidae	Ladybirds
Arthropoda	Hexapoda	Insecta	Coleoptera	Corylophidae	Minute fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Cryptophagidae	Silken fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Curculionidae	Weevils
Arthropoda	Hexapoda	Insecta	Coleoptera	Dermestidae	Carrion beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Elateridae	Click beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Latridiidae	Mildew beetles

PHYLUM	SUBPHYLUM	CLASS	ORDER	FAMILY	COMMON NAME
Arthropoda	Hexapoda	Insecta	Coleoptera	Leiodidae	Small carrion beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Melandryidae	False darkling beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Melyridae	Leaping beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Mycetophagidae	Hairy fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Oedemeridae	Lax beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Ptiliidae	Feather-winged beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Scarabaeidae	Scarabs
Arthropoda	Hexapoda	Insecta	Coleoptera	Scirtidae	Marsh beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Scydmaenidae	Stone beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Staphylinidae	Rove beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Tenebrionidae	Darkling beetles
Arthropoda	Hexapoda	Insecta	Diptera		True flies
Arthropoda	Hexapoda	Insecta	Thysanoptera		Thrips

Appendix 2

COLEOPTERA TAXA FOUND AT DEEP STREAM AND MOUNT BENGER

Native/adventive status, trophic group and presence at Deep Stream (DS) and Mount Benger (MB) are indicated.

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE	
				DS	MB
Anthicidae	*Anthicus otagoensis* Bates	Native	Carnivore	×	
Anthicidae	*Anthicus* sp. cf. *minor* Broun	Native	Carnivore	×	
Anthribidae	*Euciodes suturalis* Pascoe	Adventive	Herbivore	×	
Archeocryptidae	*Archeocrypticus topali* Kaszab	Adventive	Fungivore		×
Byrrhidae	Byrrhidae MB larva sp. 1	Native	Herbivore	×	×
Byrrhidae	Byrrhidae MB larva sp. 2	Native	Herbivore		×
Byrrhidae	Byrrhidae MB larva sp. 3	Native	Herbivore	×	×
Byrrhidae	Byrrhidae MB larva sp. 4	Native	Herbivore		×
Byrrhidae	*Microchaetes* DS sp. 1	Native	Herbivore	×	×
Byrrhidae	*Microchaetes* MB sp. 1	Native	Herbivore		×
Byrrhidae	*Synorthus* DS sp. 1	Native	Herbivore	×	×
Byrrhidae	*Synorthus* MB sp. 1	Native	Herbivore		×
Byrrhidae	*Synorthus* MB sp. 2	Native	Herbivore		×
Cantharidae	*Asilis subnuda* Broun	Native	Carnivore	×	
Cantharidae	Cantharidae DS larva sp. 1	Native	Carnivore	×	×
Carabidae	*Anchonemus otagoensis* (Bates)	Native	Carnivore	×	×
Carabidae	*Bembidion* MB sp. 1	Native	Carnivore		×
Carabidae	Carabidae DS larva sp. 1	Native	Carnivore	×	
Carabidae	Carabidae DS larva sp. 2	Native	Carnivore	×	×
Carabidae	Carabidae DS larva sp. 3	Native	Carnivore	×	
Carabidae	Carabidae DS larva sp. 4	Native	Carnivore	×	×
Carabidae	Carabidae DS larva sp. 5	Native	Carnivore	×	
Carabidae	Carabidae MB larva sp. 1	Native	Carnivore		×
Carabidae	Carabidae MB larva sp. 2	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 3	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 4	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 5	Native	Carnivore	×	×
Carabidae	*Demetrida moesta* Sharp	Native	Carnivore	×	×
Carabidae	*Dicrochile novaezelandiae* (Fairmaire)	Native	Carnivore	×	
Carabidae	*Holcaspis placida* Broun	Native	Carnivore	×	
Carabidae	*Holcaspis punctigera* Broun	Native	Carnivore	×	×
Carabidae	*Mecodema minax* Britton	Native	Carnivore		×
Carabidae	*Mecyclothorax rotundicollis* (White)	Native	Carnivore	×	
Carabidae	*Megadromus fultoni/meritus*	Native	Carnivore	×	
Carabidae	*Notagonum* sp. cf. *feredayi* (Bates)	Native	Carnivore	×	
Carabidae	*Oopterus* DS sp. 1	Native	Carnivore	×	
Carabidae	*Oopterus* MB sp. 1	Native	Carnivore		×
Carabidae	*Oregus aereus* White	Native	Carnivore	×	×
Carabidae	*Pelodiaetus* MB sp. 1	Native	Carnivore		×

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE	
				DS	MB
Carabidae	*Scopodes cognatus* Broun	Native	Carnivore		×
Carabidae	*Scopodes edwardsi* Bates	Native	Carnivore	×	
Carabidae	*Scopodes fossulatus* (Blanchard)	Native	Carnivore	×	×
Cerambycidae	Cerambycidae DS larva sp. 1	Native	Herbivore	×	
Cerambycidae	*Ptinosoma spinicolle* Broun	Native	Herbivore	×	
Cerambycidae	*Somatidia* DS sp. 1	Native	Herbivore	×	
Chrysomelidae	*Adoxia pygidialis* (Broun)	Native	Herbivore	×	×
Chrysomelidae	*Allocharis* DS sp. 1	Native	Herbivore		×
Chrysomelidae	*Allocharis limbata* Broun	Native	Herbivore		×
Chrysomelidae	*Allocharis* MB sp. 1	Native	Herbivore	×	×
Chrysomelidae	*Chaetocnema* DS sp. 1	Native	Herbivore	×	×
Chrysomelidae	*Chaetocnema* DS sp. 2	Native	Herbivore	×	
Chrysomelidae	*Chaetocnema* MB sp. 1	Native	Herbivore		×
Chrysomelidae	*Chaetocnema* MB sp. 2	Native	Herbivore		×
Chrysomelidae	Chrysomelidae DS larva sp. 1	Native	Herbivore	×	
Chrysomelidae	Chrysomelidae DS sp. 2	Native	Herbivore	×	
Chrysomelidae	Galerucinae MB larva sp. 1	Native	Herbivore	×	×
Chrysomelidae	Galerucinae MB larva sp. 2	Native	Herbivore	×	×
Coccinellidae	?*Rhizobius* MB sp. 2	Native	Carnivore	×	
Coccinellidae	?*Rhizobius* MB sp. 3	Native	Carnivore		×
Coccinellidae	?*Rhizobius* MB sp. 4	Native	Carnivore		×
Coccinellidae	*Coccinella 11-punctata* L.	Adventive	Carnivore	×	×
Coccinellidae	*Coccinella leonina* F.	Adventive	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 1	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 2	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 3	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 4	Native	Carnivore	×	
Coccinellidae	Coccinellidae DS larva sp. 5	Adventive	Carnivore	×	×
Coccinellidae	Coccinellidae DS sp. 1	Native	Carnivore	×	
Coccinellidae	Coccinellidae DS sp. 2	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS sp. 3	Native	Carnivore	×	
Coccinellidae	Coccinellidae MB larva sp. 1	Native	Carnivore		×
Coccinellidae	Coccinellidae MB sp. 1	Native	Carnivore		×
Coccinellidae	Coccinellidae MB sp. 4	Native	Carnivore		×
Coccinellidae	*Veronicobius* sp. cf. *tristis*	Native	Carnivore	×	×
Corylophidae	Corylophidae DS larva sp. 1	Native	Fungivore	×	
Corylophidae	Corylophidae MB larva sp. 1	Native	Fungivore		×
Corylophidae	*Holopsis* DS sp. 1	Native	Fungivore	×	×
Corylophidae	*Holopsis* DS sp. 2	Native	Fungivore	×	×
Cryptophagidae	*Antarcticotectus silvanus*	Native	Fungivore	×	×
Cryptophagidae	Cryptophagidae DS larva sp. 1	Native	Fungivore	×	
Cryptophagidae	*Cryptophagus* DS sp. 1	Adventive	Fungivore	×	
Cryptophagidae	*Cryptophagus* DS sp. 2	Adventive	Fungivore	×	×
Curculionidae	?*Crisius* MB sp. 2	Native	Herbivore		×
Curculionidae	*Athor arcifer* Broun	Native	Herbivore	×	
Curculionidae	*Baeosomus amplus* Broun	Native	Herbivore	×	×
Curculionidae	*Baeosomus* DS sp. 4	Native	Herbivore	×	×
Curculionidae	*Baeosomus* DS sp. 6	Native	Herbivore	×	×
Curculionidae	*Baeosomus* MB sp. 1	Native	Herbivore	×	×

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE DS	MB
Curculionidae	*Baeosomus rugosus* Broun	Native	Herbivore	×	×
Curculionidae	*Baeosomus* sp. cf. *angustus* (Broun)	Native	Herbivore	×	×
Curculionidae	*Baeosomus* sp. cf. *crassipes* (Broun)	Native	Herbivore	×	×
Curculionidae	*Catoptes cuspidatus* (Broun)	Native	Herbivore	×	×
Curculionidae	*Catoptes dispar* Broun	Native	Herbivore		×
Curculionidae	*Catoptes* DS sp. 1	Native	Herbivore	×	×
Curculionidae	*Catoptes robustus* Sharp	Native	Herbivore	×	
Curculionidae	Cryptorhynchini MB sp. 1	Native	Herbivore		×
Curculionidae	Curculionidae DS larva sp. 2	Native	Herbivore	×	
Curculionidae	Curculionidae MB larva sp. 1	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 2	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 3	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 4	Native	Herbivore		×
Curculionidae	*Eugnomus dispar* (Broun)	Native	Herbivore	×	
Curculionidae	*Eugnomus durvillei* Schonherr	Native	Herbivore	×	×
Curculionidae	*Gromilus* DS sp. 1	Native	Herbivore	×	
Curculionidae	*Gromilus* DS sp. 2	Native	Herbivore	×	
Curculionidae	*Gromilus impressus* (Broun)	Native	Herbivore	×	
Curculionidae	*Gromilus* MB sp. 1	Native	Herbivore		×
Curculionidae	*Gromilus* MB sp. 2	Native	Herbivore		×
Curculionidae	*Irenimus curvus* Barratt & Kuschel	Native	Herbivore	×	×
Curculionidae	*Irenimus posticalis* (Broun)	Native	Herbivore	×	
Curculionidae	*Irenimus stolidus* Broun	Native	Herbivore	×	×
Curculionidae	*Listronotus bonariensis* (Kuschel)	Adventive	Herbivore	×	×
Curculionidae	*Nestrius* DS sp. 1	Native	Herbivore		×
Curculionidae	*Nestrius* MB sp. 1	Native	Herbivore		×
Curculionidae	*Nestrius* MB sp. 2	Native	Herbivore		×
Curculionidae	*Nestrius* MB sp. 3	Native	Herbivore		×
Curculionidae	*Nestrius* MB sp. 4	Native	Herbivore		×
Curculionidae	*Nicaeana cinerea* Broun	Native	Herbivore	×	×
Curculionidae	*Otiorhynchus ovatus* L.	Adventive	Herbivore		×
Curculionidae	*Peristoreus ?sexmaculatus* (Broun)	Native	Herbivore	×	
Curculionidae	*Peristoreus insignis* (Broun)	Native	Herbivore	×	×
Curculionidae	*Peristoreus* MB sp. 2	Native	Herbivore		×
Curculionidae	*Peristoreus veronicae* (Broun)	Native	Herbivore	×	
Curculionidae	*Rhopalomerus alternans* (Broun)	Native	Herbivore		×
Curculionidae	*Sitona discoideus* Gyllenhal	Adventive	Herbivore	×	
Curculionidae	*Tanysoma angustulum* Broun	Native	Herbivore	×	
Curculionidae	*Trichosirocalus horridus* (Panzer)	Adventive	Herbivore		×
Curculionidae	*Trinodicalles* MB sp. 1	Native	Herbivore		×
Dermestidae	*Anthrenocerus australis* (Hope)	Adventive	Carrion	×	
Dermestidae	Dermestidae DS larva sp. 2	Native	Carrion	×	
Dermestidae	Dermestidae DS larva sp. 3	Native	Carrion	×	
Dermestidae	Dermestidae MB larva sp. 1	Native	Carrion	×	×
Dermestidae	*Reesa vespulae* (Milliron)	Adventive	Carrion	×	×
Elateridae	*Betarmonides* DS sp. 1	Native	Herbivore	×	
Elateridae	Elateridae DS larva sp. 1	Native	Herbivore	×	
Elateridae	Elateridae DS sp. 1	Native	Herbivore	×	
Elateridae	Elateridae MB larva sp. 1	Native	Herbivore	×	×

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE	
				DS	MB
Elateridae	Elateridae MB larva sp. 2	Native	Herbivore	×	×
Elateridae	Elateridae MB sp. 1	Native	Herbivore	×	×
Elateridae	Elateridae MB sp. 2	Native	Herbivore		×
Elateridae	*Elatichrosis* sp. cf. *‘castanea’* (Broun)	Native	Herbivore	×	×
Erotylidae	*Loberus anthracinus* (Broun)	Native	Fungivore		×
Latridiidae	?*Corticaria* DS sp. 4	Native	Fungivore	×	×
Latridiidae	*Aridius bifasciatus* (Reitter)	Adventive	Fungivore	×	×
Latridiidae	*Cartodere* DS sp. 1	Adventive	Fungivore	×	
Latridiidae	*Corticaria formicaephila* (Broun)	Native	Fungivore	×	×
Latridiidae	*Corticaria serrata* (Paykull)	Adventive	Fungivore	×	×
Latridiidae	Latridiidae DS larva sp. 1	Native	Fungivore	×	
Latridiidae	*Melanopthalma* DS sp. 2	Native	Fungivore	×	
Latridiidae	*Melanopthalma gibbosa* (Herbst)	Native	Fungivore	×	×
Leiodidae	*Inocatops compactus* (Broun)	Native	Fungivore	×	×
Leiodidae	*Isocolon modestum* Broun	Native	Fungivore	×	
Leiodidae	Leiodidae DS larva sp. 1	Native	Fungivore	×	
Melandryidae	*Hylobia* MB sp. 1	Native	Fungivore		×
Melyridae	*Arthracanthus* DS sp. 1	Native	Herbivore	×	×
Melyridae	Melyridae DS larva sp. 1	Native	Carnivore	×	×
Mycetophagidae	Mycetophagidae DS sp. 1	Native	Fungivore	×	
Mycetophagidae	Mycetophagidae MB larva sp. 1	Native	Fungivore		×
Mycetophagidae	Mycetophagidae MB larva sp. 2	Native	Fungivore		×
Mycetophagidae	*Typhaea sterocorea* L.	Adventive	Fungivore		×
Oedemeridae	*Thelyphassa nemoralis* (Broun)	Native	Fungivore		×
Ptiliidae	*Ptinella* DS sp. 1	Native	Fungivore	×	×
Ptiliidae	*Ptinella* DS sp. 2	Native	Fungivore	×	×
Ptiliidae	*Ptinella* MB sp. 1	Native	Fungivore	×	×
Scarabaeidae	*Costelytra zealandica* (White)	Native	Herbivore	×	
Scarabaeidae	*Odontria striata* White	Native	Herbivore	×	
Scarabaeidae	*Odontria striata* White larva	Native	Herbivore	×	×
Scarabaeidae	*Pyronota* DS larva sp. 1	Native	Herbivore	×	
Scarabaeidae	*Pyronota festiva* (F.)	Native	Herbivore	×	×
Scirtidae	Scirtidae MB sp. 1	Native	Herbivore		×
Scirtidae	Scirtidae MB sp. 2	Native	Herbivore		×
Scolytidae	*Hylastes ater* (Paykull)	Adventive	Herbivore		×
Scraptiidae	*Nothotelus* DS sp. 1	Native	Herbivore	×	
Scydmaenidae	Scydmaenidae DS larva sp. 1	Native	Carnivore	×	×
Scydmaenidae	Scydmaenidae DS larva sp. 2	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae DS sp. 1	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae DS sp. 2	Native	Carnivore	×	×
Scydmaenidae	Scydmaenidae DS sp. 3	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae MB larva sp. 1	Native	Carnivore		×
Staphylinidae	*Agnostethus* DS sp. 1	Native	Carnivore	×	
Staphylinidae	*Agnostethus* DS sp. 2	Native	Carnivore	×	
Staphylinidae	*Agnostethus* MB sp. 1	Native	Carnivore		×
Staphylinidae	Aleocharinae Cass sp. 1	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 1	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 10	Native	Carnivore		×
Staphylinidae	Aleocharinae DS sp. 13	Native	Carnivore	×	

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE	
				DS	MB
Staphylinidae	Aleocharinae DS sp. 2	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 3	Native	Carnivore	×	
Staphylinidae	Aleocharinae DS sp. 4	Native	Carnivore	×	
Staphylinidae	Aleocharinae DS sp. 5	Native	Carnivore	×	
Staphylinidae	Aleocharinae DS sp. 6	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 7	Native	Carnivore	×	
Staphylinidae	Aleocharinae DS sp. 8	Native	Carnivore	×	
Staphylinidae	Aleocharinae DS sp. 9	Native	Carnivore	×	×
Staphylinidae	Aleocharinae MB sp. 1	Native	Carnivore	×	×
Staphylinidae	Aleocharinae MB sp. 2	Native	Carnivore		×
Staphylinidae	Aleocharinae MB sp. 3	Native	Carnivore		×
Staphylinidae	Aleocharinae MB sp. 4	Native	Carnivore	×	×
Staphylinidae	Aleocharinae MB sp. 5	Native	Carnivore		×
Staphylinidae	Aleocharinae MB sp. 6	Native	Carnivore		×
Staphylinidae	*Anabaxis* Tukino sp. 1	Native	Carnivore	×	×
Staphylinidae	*Eupines* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	*Eupines* MB sp. 1	Native	Carnivore		×
Staphylinidae	Habrocerinae DS sp. 1	Native	Carnivore	×	
Staphylinidae	*Hyperomma* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	*Maorothius* DS sp. 1	Native	Carnivore	×	
Staphylinidae	*Microsilpha* DS sp. 2	Native	Carnivore	×	
Staphylinidae	*Microsilpha* DS sp. 3	Native	Carnivore	×	
Staphylinidae	*Paraphytopus* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	*Protopristus* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	*Protopristus* DS sp. 2	Native	Carnivore	×	×
Staphylinidae	*Protopristus* DS sp. 3	Native	Carnivore	×	×
Staphylinidae	*Protopristus* MB sp. 1	Native	Carnivore	×	×
Staphylinidae	*Pselaphaulax* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS larva sp. 1	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 1	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 2	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 3	Native	Carnivore	×	
Staphylinidae	Pselaphinae DS sp. 4	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 5	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 6	Native	Carnivore	×	
Staphylinidae	Pselaphinae DS sp. 7	Native	Carnivore	×	×
Staphylinidae	Pselaphinae DS sp. 9	Native	Carnivore	×	
Staphylinidae	Pselaphinae MB larva sp. 1	Native	Carnivore	×	×
Staphylinidae	Pselaphinae MB larva sp. 2	Native	Carnivore	×	×
Staphylinidae	Pselaphinae MB sp. 1	Native	Carnivore		×
Staphylinidae	Pselaphinae MB sp. 2	Native	Carnivore		×
Staphylinidae	Pselaphinae MB sp. 3	Native	Carnivore		×
Staphylinidae	Pselaphinae MB sp. 4	Native	Carnivore	×	×
Staphylinidae	Pselaphinae MB sp. 5	Native	Carnivore	×	×
Staphylinidae	Pselaphinae Tukino sp. 2	Native	Carnivore	×	
Staphylinidae	*Pselaphophus atriventris* (Westwood)	Adventive	Carnivore		×
Staphylinidae	*Pselaphophus* MB sp. 1	Adventive	Carnivore		×
Staphylinidae	'*Quedius*' DS sp. 1	Adventive	Carnivore		×
Staphylinidae	'*Quedius*' MB sp. 1	Adventive	Carnivore		×

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE DS	MB
Staphylinidae	*Sagola* DS sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 2	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 3	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 6	Native	Carnivore	×	×
Staphylinidae	Staphylinidae DS larva sp. 8	Native	Carnivore	×	
Staphylinidae	Staphylinidae MB larva sp. 1	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 2	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 3	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 4	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 5	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 6	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 7	Native	Carnivore	×	×
Staphylinidae	Staphylininae DS sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylininae DS sp. 2	Native	Carnivore	×	
Staphylinidae	Tachyporinae MB sp. 1	Native	Carnivore		×
Staphylinidae	*Tachyporus nitidulus* (F.)	Adventive	Carnivore	×	
Staphylinidae	*Zealandius* DS sp. 1	Native	Carnivore	×	×
Staphylinidae	*Zealandius* DS sp. 2	Native	Carnivore	×	×
Tenebrionidae	*Lorelus tarsalis* Broun	Native	Herbivore	×	
Tenebrionidae	Tenebrionidae DS larva sp. 1	Native	Herbivore	×	×
Tenebrionidae	Tenebrionidae DS larva sp. 2	Native	Herbivore	×	×
Tenebrionidae	*Zeadelium aeratum* (Broun)	Native	Herbivore	×	
Tenebrionidae	*Zeadelium chalmeri* (Broun)	Native	Herbivore		×
Tenebrionidae	*Zeadelium hudsoni* (Broun)	Native	Herbivore	×	×
Tenebrionidae	*Zeadelium senile* Watt	Native	Herbivore	×	×
Tenebrionidae	*Zeadelium* sp. cf. *nigritulum* (Broun)	Native	Herbivore		×
Trogossitidae	Trogossitidae MB sp. 1	Native	Fungivore		×
Zopheridae	*Bitoma morosa* (Broun)	Native	Fungivore	×	
Zopheridae	*Notocoxellus* MB sp. 1	Native	Fungivore		×
Zopheridae	*Pristoderus* DS sp. 1	Native	Fungivore	×	
Zopheridae	*Pristoderus* MB sp. 3	Native	Fungivore	×	

Appendix 3

NOTES ON IDENTIFICATION AND ECOLOGY OF SOME SPECIES

A3.1   Mollusca

The snail fauna has been examined by Frank Climo (c/- Te Papa Museum). Despite being relatively low in abundance, the fauna was of great interest, possibly because it has been so poorly collected from tussock grassland areas such as our sites in the past. The collection has extended the range of some species and added considerably to the quantity of known specimens for some species. Notably, *Flammulina* n. sp. (Amphodoxinae) was known previously from only two specimens from Governor's Bush, Mt Cook; this species was found to be well represented in the material from Deep Stream.

A3.2   Amphipoda

Terrestrial amphipods are litter dwellers, feeding on decaying organic material, and dependent upon a moist, humid habitat. It has been noted by Friend & Richardson (1986) that only the hardiest groups of terrestrial amphipods have extended their range from forest into grassland environments. The talitrid *Makawe* (= *Orchestia*) *hurleyi* (Duncan) is known to have successfully colonised eastern South Island grassland and can reach densities of 300/m² in disturbed grassland (Duncan 1969), although it is limited to areas where rainfall is above about 600 mm per annum. Identification of the species most commonly found in the current study has not been confirmed, but is likely to be *Parorchestia tenuis* (Dana), given the characteristics described by Duncan (1994).

A3.3   Hymenoptera: Formicidae

In our study, the ant fauna was represented by three species, which were present at both sites. The predominant species found was the widespread endemic *Monomorium antarcticum* (Fr. Smith), which is a generalist feeder, preying on small insects, harvesting small seeds, and 'milking' homopterans (Don 2007). The population density reduction following fire could be attributable to reduced prey items and seed availability, since it would be expected that in the event of fire, population survival in subterranean nests (to which the highly mobile individuals would most likely retreat) might be quite high. The other two species found were the endemic *Huberia striata* (Fr. Smith), and the adventive species *Prolasius advena* (Fr. Smith), both of which were present in comparatively low numbers.

A3.4   Hemiptera: Pseudococcidae

Although a full identification of all pseudococcid material has not been carried out, a subsample was examined, within which three species were identified (Rosa Henderson, Landcare Research, pers. comm. 2000). These were *Ventrispina otagoensis* (Brittin), *Laminicoccus eastopi* Cox, and *Balanococcus danthoniae* (Morrison). *Ventrispina otagoensis* is found throughout New Zealand and has been associated with Poaceae, Rosaceae and mosses. *Laminicoccus eastopi* has been recorded from *Chionochloa* spp., and *B. danthoniae* from a number of grass species where it feeds in the leaf sheaths.

A3.5   Thysanoptera

At Deep Stream, the predominant species of Thysanoptera found was *Aptinothrips rufus* (Haliday), an exotic, cosmopolitan species known as the grass thrips. This species has a wide plant host range (Mound & Walker 1982) and was mainly responsible for the 'outbreak' in thrips densities that occurred 1–2 years post-burn. Also present but far less abundant were *Aptinothrips stylifer* Trybom, which is well known from South Island tussock grassland; *Chirothrips manicatus* (Haliday), known as Timothy thrips, which is associated with exotic and native grasses; the exotic tubuliferan spore-feeding *Nesothrips propinquus* (Bagnall), which is also well known from tussock grassland; and the long-tailed tubuliferan *Baenothrips moundi* (Stannard), another exotic species from Australia that feeds on fungal hyphae in leaf litter (Mound & Walker 1982). At Mount Benger, the same *Aptinothrips* species were present, as well as two Australian species that were recorded from sub-alpine tussock grass bases, *Carientothrips badius* (Hood) and *Emprosthiothrips* sp. The New Zealand flower thrips, *Thrips obscuratus* (Crawford), was also present; this is a New Zealand native species found in inflorescences of a wide range of species and sometimes considered a pest. Lawrence Mound (CSIRO, Canberra), who examined some of the thrips material from these sites, commented that he was surprised to see so few native species.

A3.6   Coleoptera: Ptiliidae

Taxonomy of the Ptiliidae, a family of minute beetles commonly known as feather-wing beetles, was revised in 1982 (Johnson 1982). To date, 56 species in 13 genera have been recognised from New Zealand. Very little information is given in the revision about the biology or ecology of the group, but they are believed to be fungivores, feeding on fungal spores and hyphae (Lawrence & Britton 1994; Klimaszewski & Watt 1997). Published observations have shown that ptiliids tend to be found in very moist environments (haystack bottoms, compost, litter, moss, under bark, etc.). One species has been found only in deeply set pitfall traps, suggesting that it lives in the soil. In the current study, the species found were mainly present in tussock samples at the two sites and seem best to fit the genus *Ptinella*, which is a large genus with species that are typically difficult to differentiate. No members of this genus seem to have been associated previously with *Chionochloa* species. However, Johnson (1975) had recorded species occurring on *Poa* tussock bases and extracted from tussock leaf mould on subantarctic islands.
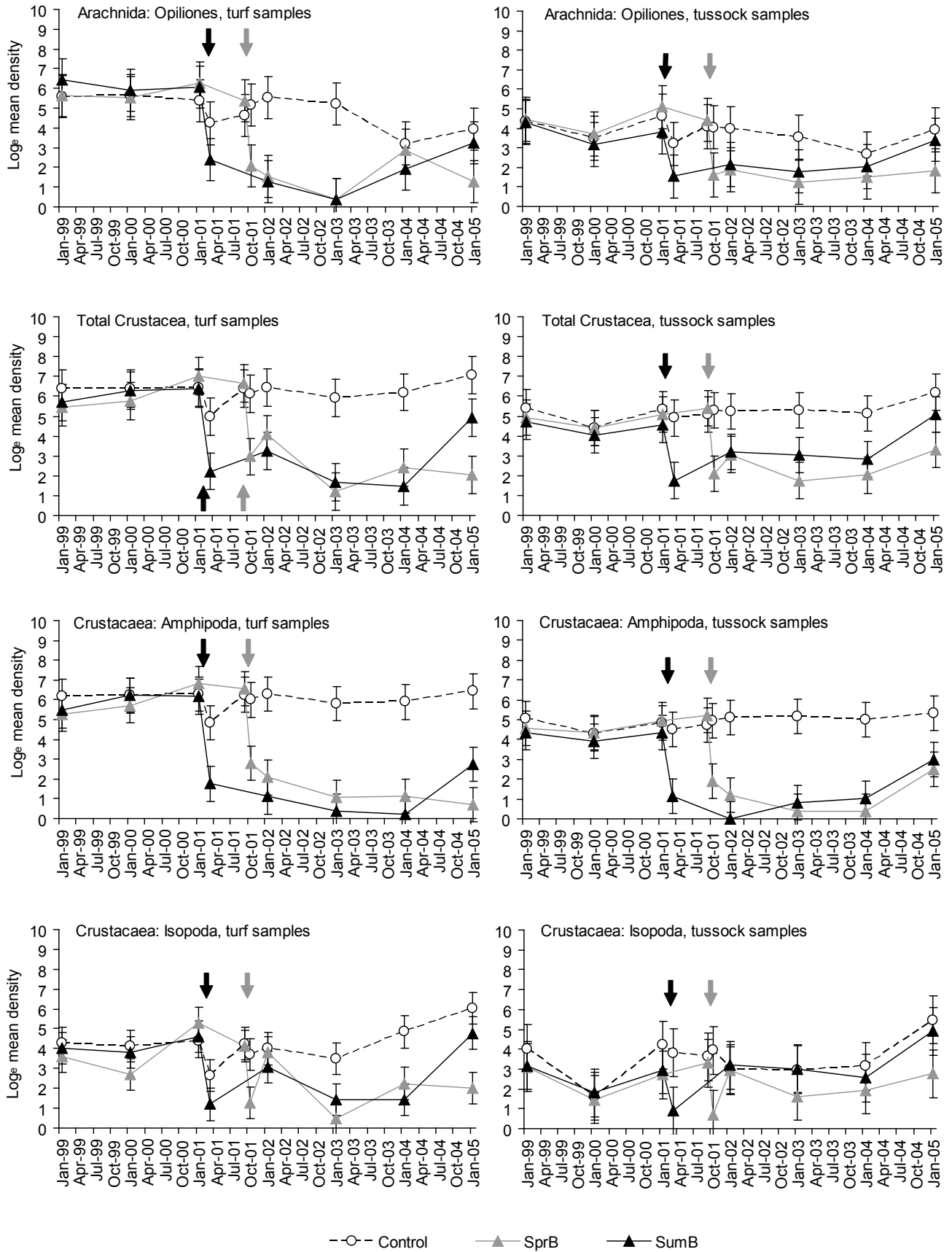
Appendix 4

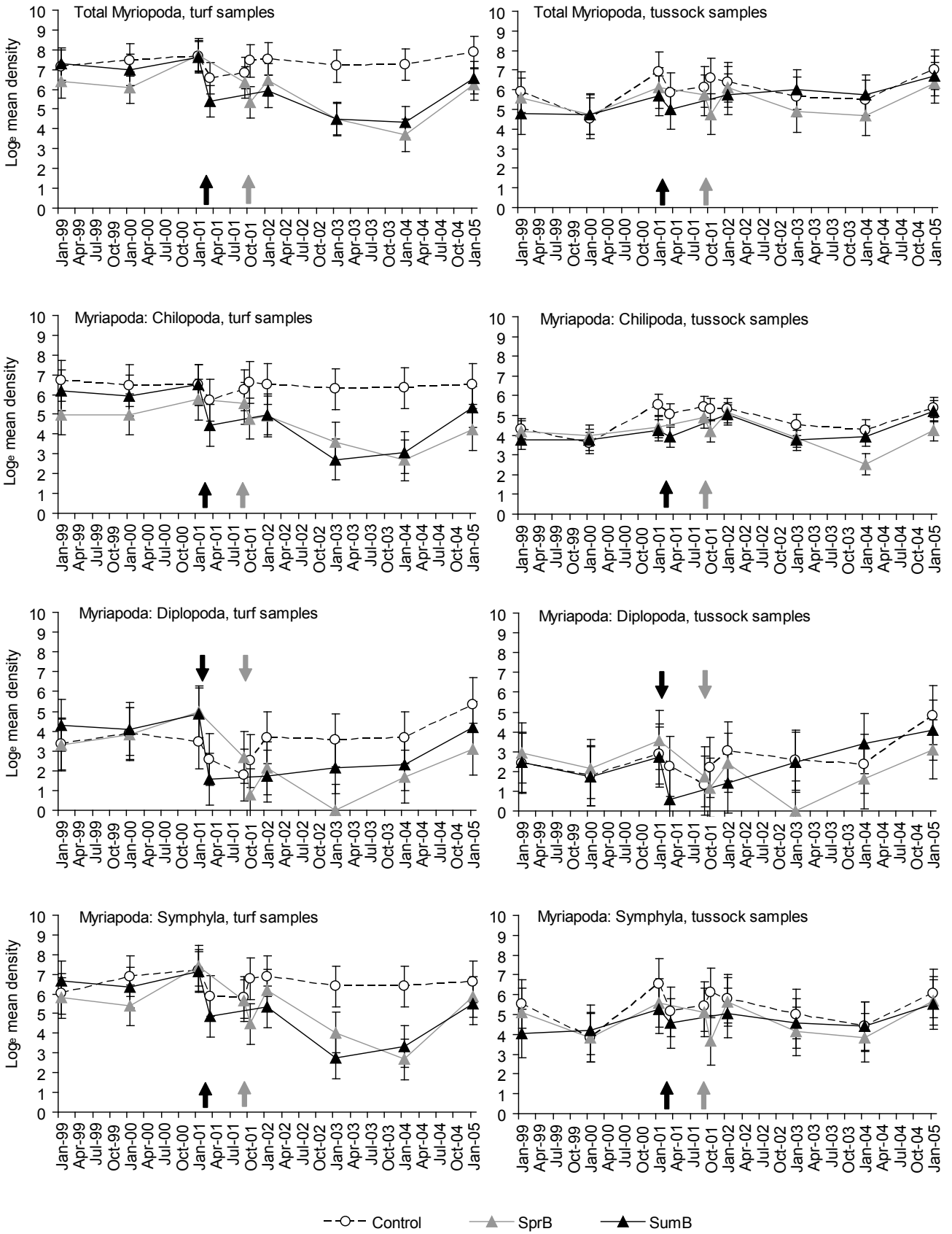## MEAN DENSITY OF INVERTEBRATE GROUPS AT DEEP STREAM

Graphs show the mean density (number individuals/m^2) of invertebrate groups present in control, spring-burnt (SprB) and summer-burnt (SumB) plots. Density is expressed as log$_e$ mean density throughout the study period. Error bars represent 2 SEMs. Arrows indicate summer (black arrow) and spring (grey arrow) burn dates.
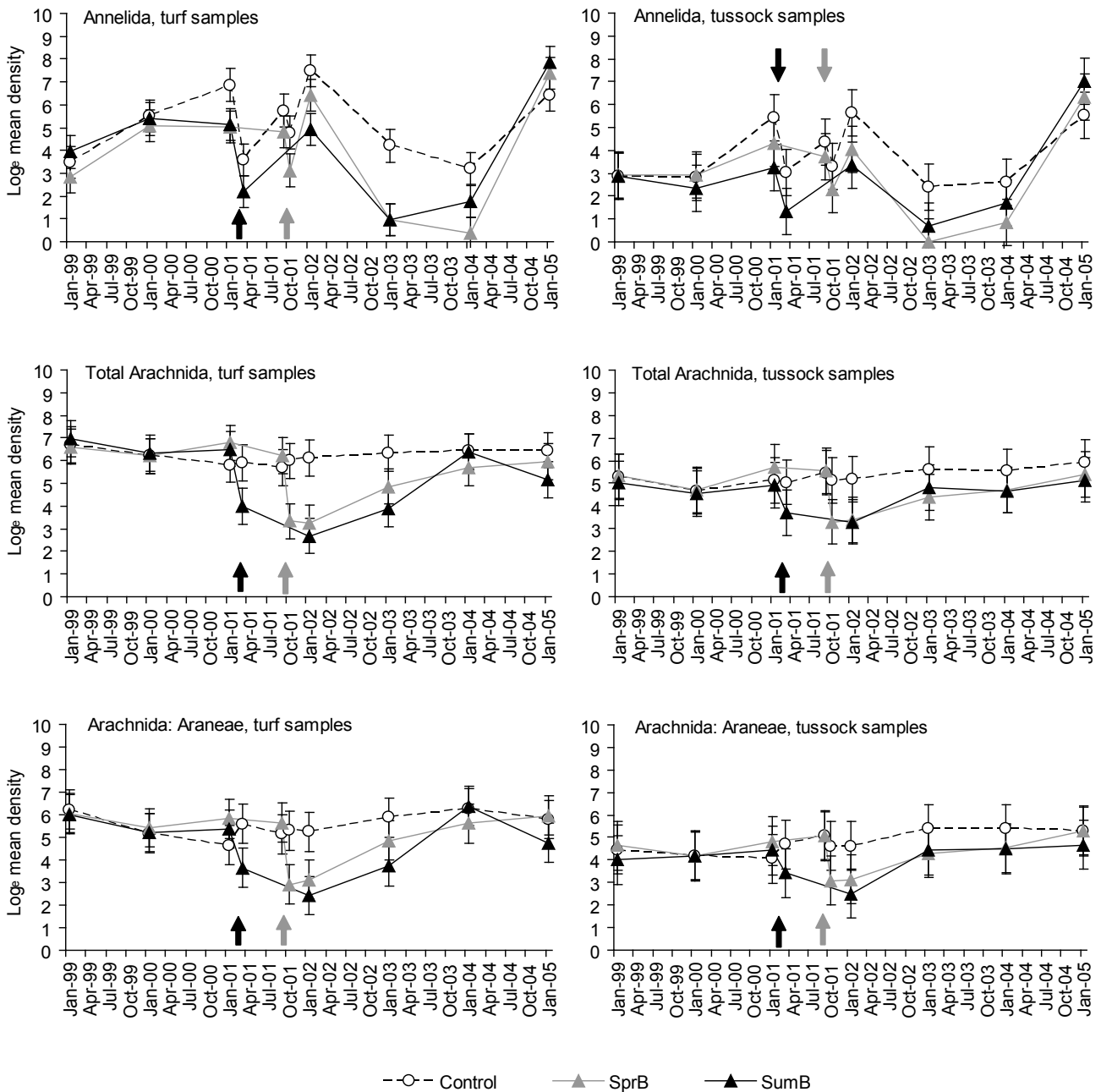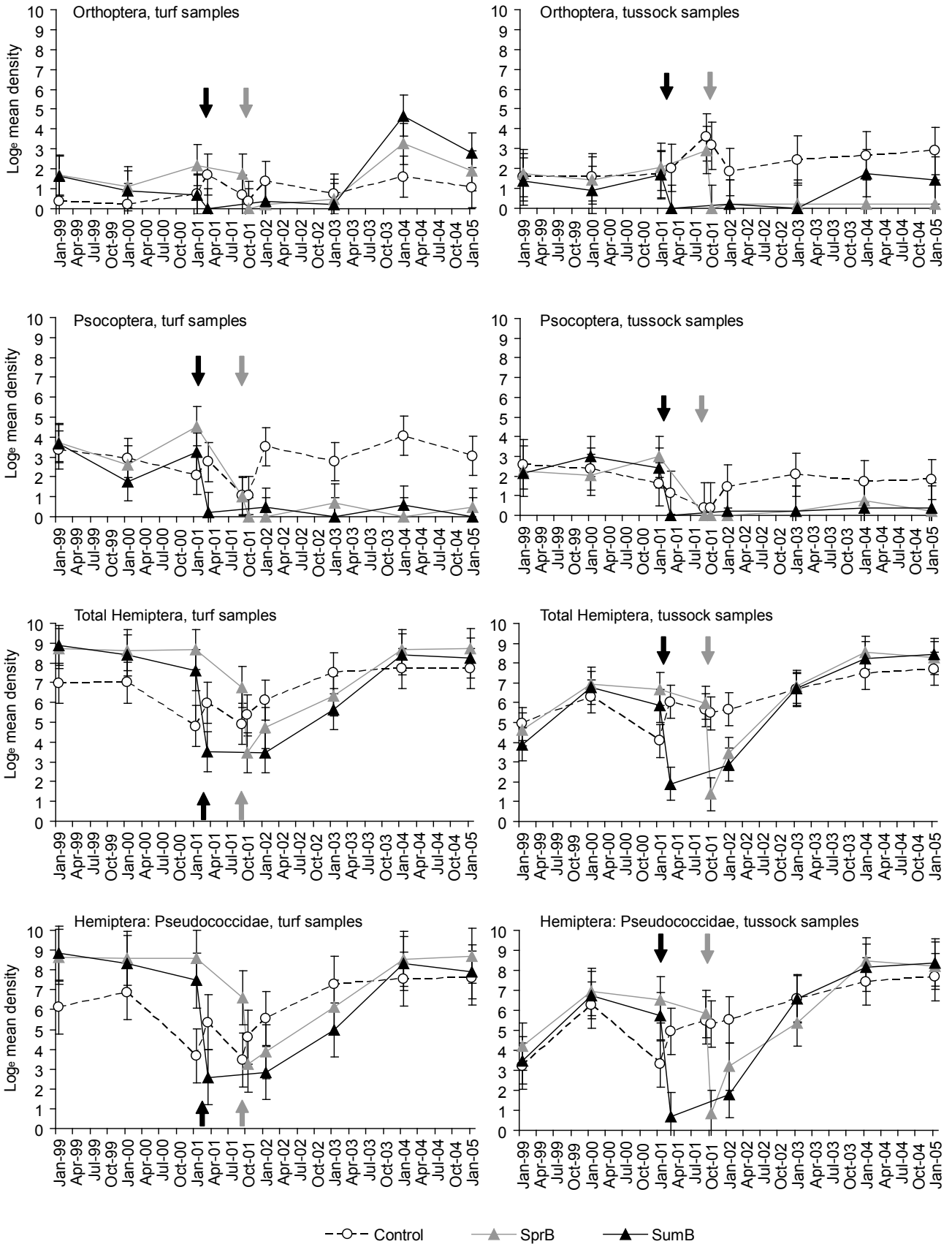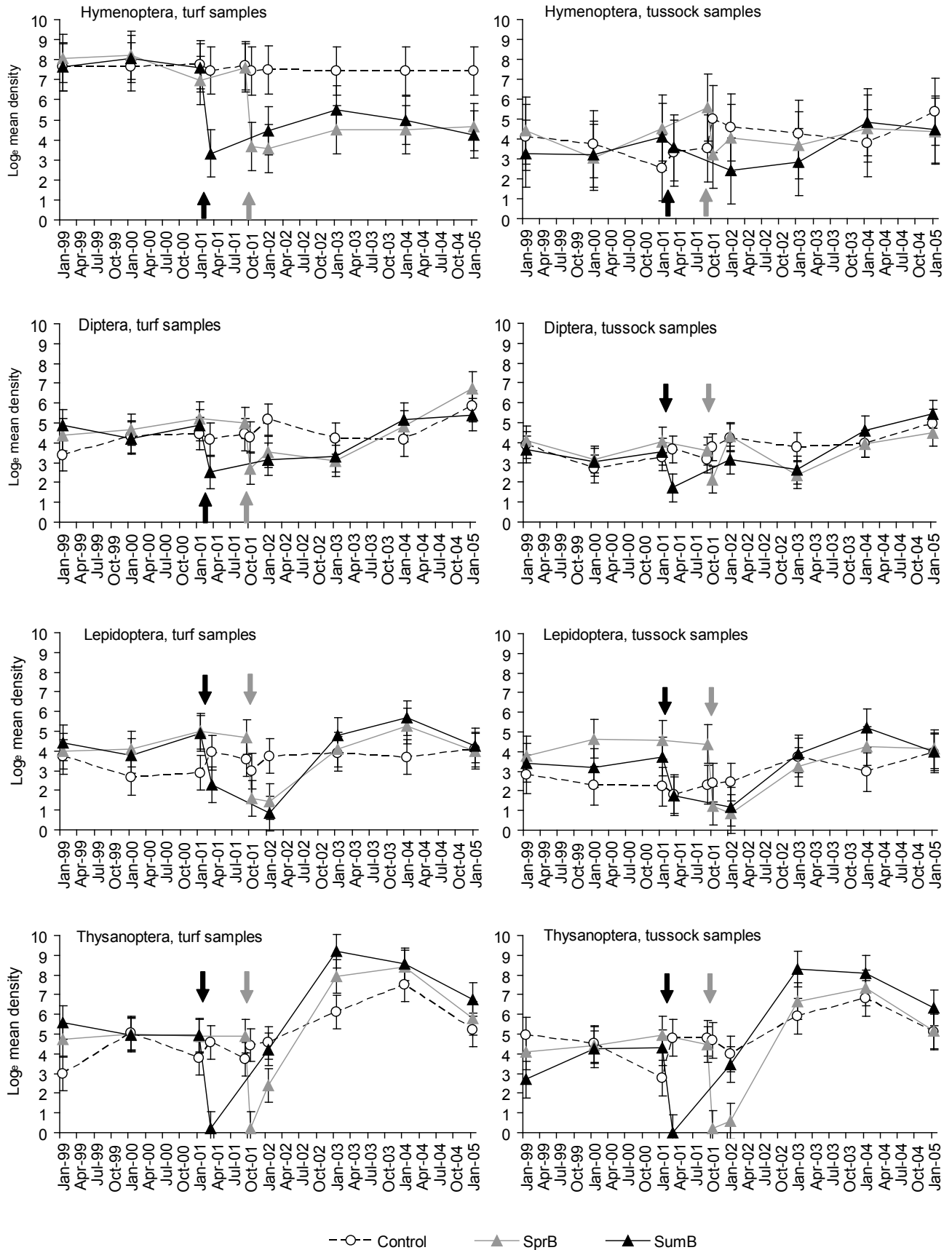
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Appendix 5

Graphs show the mean density (number individuals/m^2) of invertebrate groups present in control and spring-burnt (SprB) plots. Density is expressed as log$_e$ mean density throughout the study period. Error bars represent 2 SEMs. Arrow indicates the spring burn date.

Barratt et al.—Impact of fire on tussock invertebrates

Arachnida: Opiliones, turf samples

Arachnida: Opiliones, tussock samples

Total Crustacea, turf samples

Total Crustacea, tussock samples

Crustacaea: Amphipoda, turf samples

Crustacaea: Amphipoda, tussock samples

Crustacaea: Isopoda, turf samples

Crustacaea: Isopoda, tussock samples

--o-- Control   ▲ SprB

Total Myriapoda, turf samples

Total Myriapoda, tussock samples

Myriapoda: Chilopoda, turf samples

Myriapoda: Chilopoda, tussock samples

Myriapoda: Diplopoda, turf samples

Myriapoda: Diplopoda, tussock samples

Myriapoda: Symphyla, turf samples

Myriapoda: Symphyla, tussock samples

- ○ - Control   ▲ SprB

Orthoptera, turf samples

Orthoptera, tussock samples

Total Hemiptera, turf samples

Total Hemiptera, tussock samples

Hemiptera: Pseudococcidae, turf samples

Hemiptera: Pseudococcidae, tussock samples

Hymenoptera, turf samples

Hymenoptera, tussock samples

Control   SprB

Barratt et al.—Impact of fire on tussock invertebrates

Appendix 6

SUMMARY OF COLEOPTERA TAXA RECORDED AT DEEP STREAM (DS) AND MOUNT BENGER (MB)

Families represented (×) and an estimate of the numbers of genera and species are given. Where genus is not know, the number of genera is an estimate, particularly for Staphylinidae. Data do not include larvae.

FAMILY	PRESENCE		NO. GENERA			NO. SPECIES		
	DS	MB	DS	MB	TOTAL	DS	MB	TOTAL
Anthicidae	×		1	0	1	2	0	2
Anthribidae	×	×	1	1	1	1	1	1
Archeocryptidae		×	0	0	1	0	1	1
Byrrhidae	×	×	2	2	2	2	5	5
Cantharidae	×		1	1	1	1	0	1
Carabidae	×	×	10	9	13	12	10	17
Ceramabycidae	×		2	0	2	2	0	2
Chrysomelidae	×	×	4	3	4	5	7	9
Coccinellidae	×	×	3	3	3	7	8	11
Corylophidae	×	×	1	1	1	2	2	2
Cryptophagidae	×	×	2	2	2	3	2	3
Curculionidae	×	×	11	15	18	26	30	41
Dermestidae	×	×	2	2	2	2	1	2
Elateridae	×	×	4	3	5	4	3	5
Erotylidae		×	0	1	1	0	1	1
Latridiidae	×	×	5	4	5	7	5	7
Leiodidae	×	×	2	1	2	2	1	2
Melandryidae		×	0	1	1	0	1	1
Melyridae	×	×	1	1	1	1	1	1
Mycetophagidae	×	×	1	2	2	1	1	2
Oedemeridae		×	0	1	1	0	1	1
Ptiliidae	×	×	1	1	1	3	3	3
Scarabaeidae	×	×	3	2	3	3	1	3
Scirtidae		×	0	2	2	0	2	2
Scolytidae		×	0	1	1	0	1	1
Scraptiidae	×		1	0	1	1	0	1
Scydmaenidae	×	×	2	1	3	3	1	3
Staphylinidae	×	×	19*	17*	25*	46	40	61
Tenebrionidae	×	×	2	1	2	4	4	6
Trogossitidae		×	0	1	1	0	1	1
Zopheridae	×	×	1	1	3	3	1	4
Total	24	28	82	80	111	142	135	202

*   Estimate only.

How does fire affect tussock grassland invertebrates?

The impacts of spring and summer burns on tussock grassland invertebrate communities were investigated at two sites in Otago, New Zealand. The density of most taxa was initially reduced following burning. However, recovery rates in the years following the burning treatments varied between taxa. In general, herbivore populations recovered within 2–3 years of burning, whereas litter-dwelling taxa were most negatively impacted. Using Coleoptera as an indicator group, there was no evidence of an increase in the proportion of exotic species in the community following fire. Contrary to expectation, summer fires did not appear to be any more detrimental to invertebrate communities than spring fires.

New Zealand Government